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## Discovery of a Defensively Malodorous and Nocturnal Frog in the Family Dendrobatidae: Phylogenetic Significance of a New Genus and Species from the Venezuelan Andes

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## ABSTRACT

The Venezuelan skunk frog, *Aromobates nocturnus*, new genus and species, was discovered in subpáramo cloud forest at the extreme northern end of the Venezuelan Andes. Its skin produces a volatile defensive compound with a mercaptanlike odor. In this and in other traits it is unique among dendrobatiids. It is the largest species in the family; at a maximum female size of 62 mm SVL, *Aromobates* is 24–37 percent larger than the largest toxic dendrobatiids and 41 percent larger than the biggest *Colostethus*. It also is the first species def-

initely known to be nocturnal, and aquatic (vs. riparian), and to have an adductor mandibulae externus superficialis muscle. Some of the distinguishing characters of *Aromobates* that contradict previous synapomorphies for the family are judged primitive; it is symplesiomorphic with some *Colostethus* in other features of morphology and in color pattern. *Aromobates nocturnus* seems to be the most primitive living dendrobatiid and is postulated to be the sister group of all other members of the Dendrobatidae.

## RESUMEN

La rana “mapurite” (zorillo) venezolana, *Aromobates nocturnus*, género y especie nuevos, fue descubierta en el bosque nublado subpáramo al extremo septentrional de los Andes venezolanos. Su piel produce un compuesto volátil defensivo con un olor similar a mercaptano. Con esta y con otras características ella es única entre los dendrobátidos. Es la especie más grande en la familia; con el tamaño máximo de hembras de 62 mm SVL, *Aromobates* es 24–37% más grande que los mayores dendrobátidos tóxicos, y 41% más grande que los *Colostethus* mayores. *Aromobates* también

es la primera especie conocida definitivamente como nocturna y acuática (en vez de ribereña) y que posee el músculo adductor mandibulae externus superficialis. Algunas características distintivas de *Aromobates* contradicen sinapomorfías previas de la familia y se consideran como primitivas; en otros rasgos de morfología y en el patrón de coloración, *Aromobates* es symplesiomórfico con algunos *Colostethus*. *Aromobates nocturnus* parece el dendrobátido viviente más primitivo y proponemos que es la especie hermana de todos los otros miembros de la familia Dendrobatidae.

## INTRODUCTION

Faunal explorations at the northern end of the Venezuelan Andes led one of us (Paolillo) to the discovery, in 1981, of a remarkable frog. Superficial examination of the first specimens left us uncertain as to the proper familial assignment. The frogs evidently belonged to a new species having certain external characters reminiscent of the Dendrobatidae, but it was a species appreciably larger than the largest known dendrobatiids and a relationship within the catchall Leptodactylidae seemed at least possible. Furthermore, the frog was aquatic, nocturnal, and emitted an unpleasant odor when handled alive—characteristics unknown in the Dendrobatidae, although nocturnality is widespread in the Leptodactylidae, which also contains aquatic species and at least one bizarre genus (*Edalorhina*) capable of emitting a similarly unpleasant, mercaptanlike odor.

Examination of the musculature and skeleton of the new frog, however, satisfied us that it belongs in the Dendrobatidae. Late in 1987 we camped for several nights in the

cloud forest where the first frogs were found, in order to acquire additional material of what we were soon calling the “Venezuelan skunk frog” (fig. 1), which is here proposed as a new species in a new genus. We also provide evidence indicating that the new taxon is the most primitive living dendrobatiid (even if arguably highly derived in one or more traits) and that it is the sister group of all other dendrobatiids.

**ACKNOWLEDGMENTS:** For authorizing use of a 4-wheel drive field vehicle and other courtesies, we are grateful to Dr. Aldemaro Romero, Executive Director of BIOMA. We thank Drs. Maureen A. Donnelly, Linda S. Ford, Darrel R. Frost, Linda Trueb, and Richard G. Zweifel for reading and commenting on the manuscript. Dr. Trueb also volunteered time from a busy schedule to prepare the osteological drawings (figs. 7, 8, 10)—an exceptional act of friendship not acknowledged well by words alone.

**ABBREVIATIONS:** Collection abbreviations used in this paper are:



Fig. 1. Venezuelan skunk frogs, *Aromobates nocturnus*, new genus and species, shown more or less life size. **Top:** Adult female holotype (AMNH 130005) with normal dark coloration. **Middle:** Adult female paratotype (AMNH 130007) with blotched pattern. **Bottom:** Adult male paratotype (AMNH 130006) with normal pattern.

AMNH	American Museum of Natural History, New York
EBRG	Estación Biológica de Rancho Grande Museo, Maracay, Venezuela
KU	University of Kansas Museum of Nat- ural History, Lawrence
MBUCV	Universidad Central de Venezuela, Ca- racas
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

*Aromobates*, new genus

TYPE SPECIES: *Aromobates nocturnus*, new species, by present designation.

ETYMOLOGY: From the Greek *aroma* (a smell) + *bates* (a walker). Gender masculine. The second half of the name is an appropriate descriptive ending in six (of seven) other generic names currently recognized or recently proposed in the Dendrobatidae. Although the malodorous type species is primarily aquatic, it too is a “walker” under certain circumstances and the ending is therefore used for purposes of commonality among dendrobatiid names.

DEFINITION AND DIAGNOSIS: Very large dendrobatiids (females to 62 mm SVL) with a noxious odor;<sup>4</sup> nontoxic, skin alkaloids absent. The *m. adductor mandibulae externus superficialis* is usually present, both it and the *m. adductor mandibulae posterior subexternus* originating from a relatively long zygomatic ramus of the squamosal bone. Retroarticular process of mandible present but very short. Nonpedicellate, fanglike teeth present on maxillary arch. Appressed first finger nearly equal to second; third finger disc 1.3–1.6 times wider than finger; narrow fringes present on all fingers, but third finger not swollen in either sex. Feet extensively webbed, with web extending to each of the scarcely expanded toe discs (narrow along phalanges 2–3 of fourth toe). Coloration dull, often with trace of an oblique lateral stripe extending from groin part way to eye and sometimes with vague indication of pale dorsolateral stripes; a usually weak dark transverse bar or

collar across base of throat in males, collar usually absent in females. Tadpole with laterally indented oral disc, 2/3 tooth rows (second upper row narrowly broken above beak), and dextral anus, reaching a total length of at least 68 mm in stage 34; aquatic larvae in small streams. Call and type of amplexus unknown. Nocturnal.

*Aromobates* is distinguished from all other dendrobatiid genera by each of the following traits: (1) noxious odor when handled; (2) larger size, with adult males 45–52 mm SVL, adult females 53–62 mm SVL; (3) *m. adductor mandibulae externus superficialis* usually present; (4) nocturnal; (5) aquatic (vs. riparian or terrestrial).

DISTRIBUTION: Known at present only from small streams in Andean cloud forest at 2250 m elevation, in the extreme northeastern corner of the State of Trujillo, northwestern Venezuela.

REMARKS: Although *Aromobates* is proposed as a monotypic genus, we should not be surprised if additional species are eventually discovered in subpáramo habitats of the incompletely explored northern Andes of Venezuela and Colombia. The known species has nocturnal habits, presumably calls infrequently (or seasonally?), and seems partial to headwater rivulets in dense cloud forest—a combination of characteristics that, if shared, could easily cause any related species to be overlooked.

*Aromobates nocturnus*, new species

Figures 1–12, 18A, 19A

HOLOTYPE: AMNH 130005 (field no. CWM 18564), an adult female obtained by the authors November 28–30, 1987, in cloud forest at 2250 m elevation, about 2 km airline ESE Agua de Obispos, Estado Trujillo, Venezuela (9°42'N, 70°05'W<sup>5</sup>).

<sup>4</sup> Possibly owing to one of the mercaptans, a class of organosulfur compounds characterized by offensive odor at very low concentrations in air. The frog compound, however, has so far defied analysis (see Biochemistry of Skin Secretions).

<sup>5</sup> From topographic sheet 6145 II S.E. (Agua de Obispos), 1:25,000, Dirección Cartografía Nacional, Venezuela, 1965 (1st ed.). This map shows only foot or horse trails where there is now a rough 10.7 km road from La Peña to Agua de Obispos. There are inaccuracies in the topography as depicted, but the 2000-m map elevation of the village of Agua de Obispos was corroborated by altimeter, at a distance of 2.5 km by road downslope from our campsite (2320 m, 8.2 km by road from La Peña). We camped near a telecommunications tower not shown on available maps.

**PARATOPOTYPES:** EBRG 2219–2228, AMNH 129940 [skin + cleared-and-stained skeleton], USNM 287692–287695 [last spec. = cleared-and-stained skeleton], all collected by A. Paolillo in December 1981.

AMNH 130006–130049 [(130032–130034, 130036–130038 = skinned carcasses); (130035, 130039–130041, 130048–130049 = cleared-and-stained skeletons); (130042–130047 = dry skeletons)]. AMNH 130050–130051 (tadpoles). All collected by the authors November 28–30, 1987. Some specimens to be deposited in KU and MBUCV.

**ETYMOLOGY:** The Latin adjective *nocturnus* (of the night) is chosen as the species name, in reference to an activity cycle previously unknown in the Dendrobatidae, albeit commonplace among other frogs.

**DEFINITION AND DIAGNOSIS:** Same as given for the genus above. Juvenile specimens of *A. nocturnus* conceivably might be confused with certain Venezuelan species of the *collaris* group of *Colostethus*, namely *guatopoensis*, *obliterratus*, and *riveroi*, which are relatively large *Colostethus* that share with *Aromobates nocturnus* the features of a dark throat collar and extensively webbed feet. These are much smaller species, of which *C. riveroi* (the largest named *Colostethus*) attains known maximum sizes of about 38 mm snout-to-vent (SVL) in adult males and 44 mm SVL in adult females (vs. 45–52 mm in male, 53–62 mm in female *Aromobates nocturnus*). See further under Comparisons with "Collared *Colostethus*".

**MEASUREMENTS (in mm) OF HOLOTYPE:** The undissected holotype is an adult female as judged by its large size and lack of vocal slits. Length from snout to vent 61.0; tibia length between heel and outer surface of flexed knee 29.2; greatest width of body 27.0; head width between angles of jaws, and between outer edges of upper eyelids at midpoint, 23.3 and 15.4, respectively; width of interorbital area 6.5; head length from tip of snout to angle of jaw 15.0 (sagittal) or 17.8 (oblique); tip of snout to center of naris (sagittal) 2.5; center of naris to anterior edge of eye 4.3; distance between centers of nares 7.2; eye length from anterior to posterior edge 7.5; horizontal diameter of tympanum < 3 (obscure); corner of mouth to lower edge of tympanic ring 2.2;

hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger 16.6; width of disc of third finger (and width of penultimate phalanx below disc) 2.7 (1.8); width of discs (and penultimate phalanges below discs) of third and fourth toes 2.5 (2.2) and 2.6 (2.0), respectively.

## DESCRIPTION

**EXTERNAL MORPHOLOGY:** A very large dendrobatid, with females maturing by about 53 mm SVL as determined by enlarged oviducts and attaining a maximum size of about 62 mm (table 1); males attain a maximum size of about 52 mm, apparently maturing at about 44 mm SVL as determined by opened vocal slits (subadult males of 43.5 and 43.9 mm SVL had discernible but unopened vocal slits). Adult males with well-developed vocal slits; subgular vocal sac shallow, apparently not very distensible.

Dorsum and flanks coarsely granular (pebbled) in life, becoming relatively smooth in some preserved specimens; ventral skin smooth in life; cloacal opening normal, not concealed by anal sheath. Head width between outer edges upper eyelids appreciably less than width between jaw articulations. Head as wide as or narrower than body. Head width between angles of jaws 36–42 percent of SVL. Short snout sloping, rounded in profile and ventral aspect, varying from rounded (usually) to truncate in dorsal aspect. Nares situated near tip of snout and directed more or less laterally; nares visible from front and from above, not or barely visible from below; posterior rim of naris raised slightly and bearing a small rounded tubercle posterodorsally to naris. Canthus rostralis rounded; loreal region concave, sloping outward to lip. Interorbital distance appreciably wider than upper eyelid. Eye longer than snout; distance from center of naris to eye 50–68 percent of eye length. Tympanum often barely discernible, concealed dorsally and posterodorsally by postocular swelling that extends as a ridge posteriorly from eye and then posteroventrally behind tympanum nearly to upper arm.

Hand moderate size, its length (proximal edge of metacarpal tubercle to tip of longest finger) 27–31 percent of SVL; hand length 68–82 percent of head width (at jaw articu-

TABLE 1  
Size and Proportions of Adult *Aromobates nocturnus*, New Species, from the Type Locality

Character	N	Mean $\pm$ 1 SE	SD	CV (%)	Range
Snout-vent length (SVL) in mm	8♂	48.55 $\pm$ 0.96	2.72	5.61	44.7-52.3
	22♀	57.49 $\pm$ 0.50	2.36	4.11	53.4-61.6
Tibia length <sup>a</sup> /SVL	8♂	0.523 $\pm$ 0.008	0.021	4.09	0.49-0.55
	22♀	0.496 $\pm$ 0.003	0.015	3.05	0.47-0.53
Head width <sup>b</sup> /SVL	8♂	0.394 $\pm$ 0.004	0.013	3.22	0.38-0.42
	22♀	0.388 $\pm$ 0.003	0.014	3.65	0.36-0.41
Center naris to edge eye/eye length	8♂	0.560 $\pm$ 0.015	0.041	7.36	0.50-0.61
	22♀	0.600 $\pm$ 0.010	0.046	7.62	0.53-0.68
Hand length <sup>c</sup> /SVL	8♂	0.303 $\pm$ 0.002	0.007	2.25	0.29-0.31
	22♀	0.290 $\pm$ 0.002	0.009	3.26	0.27-0.31
Hand length/head width	8♂	0.768 $\pm$ 0.008	0.022	2.89	0.74-0.80
	22♀	0.749 $\pm$ 0.008	0.036	4.83	0.68-0.82
Width 3rd-finger disc/finger width below disc <sup>d</sup>	8♂	1.395 $\pm$ 0.029	0.083	5.96	1.31-1.53
	22♀	1.448 $\pm$ 0.013	0.060	4.13	1.31-1.56

<sup>a</sup> Tibia length is the shank measured from the heel to the convex surface of the knee (with limb segments flexed at right angles), roughly approximating the length of the tibiofibula.

<sup>b</sup> Greatest head width as measured between jaw articulations.

<sup>c</sup> Hand length measured from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger.

<sup>d</sup> Digit width measured near distal end of penultimate phalanx.

lations). Relative length of appressed fingers  $3 > 4 > 2 > 1$ ; appressed first finger nearly as long (rarely as long) as second, its tip usually overlapping (rarely not reaching) subdigital pad of second finger (fig. 2). Discs of all fingers moderately expanded; third finger disc 1.3-1.6 times wider than distal end of adjacent phalanx, without significant sexual dimorphism. A large circular metacarpal tubercle on median base of palm, a smaller, elliptical inner metacarpal tubercle on base of first finger, and one to three subarticular tubercles (one each on fingers 1, 2; usually two each on fingers 3, 4, but an additional small tubercle sometimes present proximal to disc on fingers 3, 4); all tubercles low, with rounded surfaces. A strong to weak fringe along medial and lateral sides of each finger; lateral fringe sometimes reduced and evident mainly along median side of finger 3; third finger not swollen in either sex.

Hind limbs relatively long, with heel of appressed limb reaching eye or slightly beyond eye; tibia 47-55 percent of SVL. Relative lengths of appressed toes  $4 > 3 > 5 > 2 > 1$ ; first toe reaching middle of subarticular tubercle of second. Toe discs not noticeably expanded, being little or no wider

than adjacent phalanx, but all with well-defined paired digital scutes above and subdigital pad below. Feet extensively webbed to base or slightly above base of each disc (fig. 2); web narrow, however, along medial and lateral edges of phalanges 2-3 of longest (4th) toe; webbing formula invariably I 1-1 II 1-1 III 1-1 IV 1-1 V;<sup>6</sup> a well-developed fringe along the outer free edges of toes 1 and 5.

<sup>6</sup> This is the notational device of Savage and Heyer (1967), as modified for general use by Myers and Duellman (1982: 6) and adopted by Savage (1987: 5-6). Roman numerals represent toes, with intervening Arabic numerals representing digital segments completely or partially free of webbing (1 = the disc [incorrectly called "pad" by some authors], which contains the first phalanx). A few writers on *Colostethus* have adopted Edwards' (1974: 6, 26) modification, in which Arabic numerals represent the number of segments connected by webbing; if this kind of formula is extended to other anurans, however, it becomes impossible to visualize relative degree of completeness of webbing without knowing the phalangeal formula or seeing a figure. We find it easier to visualize relative extent of foot webbing when the numbers of free segments (phalanges + metatarsals) are given, with "0" then being used to represent complete coverage to a digit tip. We eschew the Edwards method mainly in order to avoid having a convention for dendrobatids separate from that of other anurans.

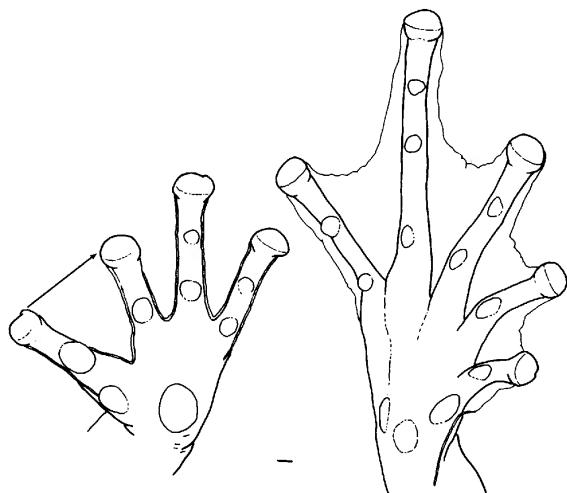


Fig. 2. Left hand and right foot of *Aromobates nocturnus* (AMNH 130005, ad. ♀ holotype). Arrow between first two fingers indicates position of digits when both are appressed.



Fig. 3. *Aromobates nocturnus* (EBRG 2222), showing traces of pale dorsolateral stripe (posterioriad from eye) and oblique lateral stripe (extending posteroverntrally from above arm to groin),  $\times 1.5$ .

One to three nonprotuberant subarticular tubercles (one each on toes 1, 2; two on 3 and 5; three on 4). Usually three metatarsal tubercles, all low and nonprotuberant, as follows: (1) a small elliptical inner metatarsal tubercle, which occasionally is fused with the following; (2) a larger rounded tubercle situated between and slightly proximal to the first (inner) and third (outer) metatarsal tubercles; and (3) a small rounded outer metatarsal tubercle. The middle metatarsal tubercle (no. 2 above) varies from an inconspicuous calloused patch in many specimens to an undeniably prominent projection in others (fig. 19A). A weak tarsal keel, on distal one-third to one-half of tarsus, is continuous with fringe on free (medial) edge of first toe; no tubercle or elevation at proximal end of tarsal keel.

**COLOR AND PATTERN:** In life, the dorsal surfaces are usually nearly uniformly dark olive (fig. 1, top and bottom) or occasionally light olive or olive brown—commonly with very weak traces of a dorsolateral stripe and incomplete oblique lateral stripe of metallic golden bronze, and with small spots or markings of the same bronze color on the upper lip and forelimbs. The dorsolateral stripe (from behind eye to end of body above thigh) and oblique lateral stripe (extending obliquely from groin to shoulder), when present, tend to be broken or present only as lines of bronze

dots (fig. 3). Occasional individuals have a blotched pattern formed by areas of dark ground color separated by areas of bronze and/or pale olive (fig. 1, middle).

The limbs are indistinctly to distinctly banded with dark or light olive and paler intervening areas of gray. The posterior surfaces of the thighs are dark colored like the dorsum, with some small and poorly defined paler areas. The ventral surfaces are finely mottled with gray and grayish white in life, being sometimes nearly uniformly gray. Adult males have a gray collar across the base of the throat anterior to the limb insertions; this marking is a darker gray than the throat and venter but is poorly defined (see fig. 4 for maximum development, fig. 18A for normal appearance). The collar is present but very faint in juvenile males and in some juvenile and adult females; it is absent in the majority of females.

The iris is grayish black, with either greenish gold or bright green flecking. The pupil is horizontal.

In preservative, the olive changes to dark brown or grayish brown and the bronze markings are grayish white. The ventral surfaces are grayish or yellowish white, usually darkened with grayish brown suffusion in a finely blotched pattern and with the gray collar remaining discernible. The undersides of

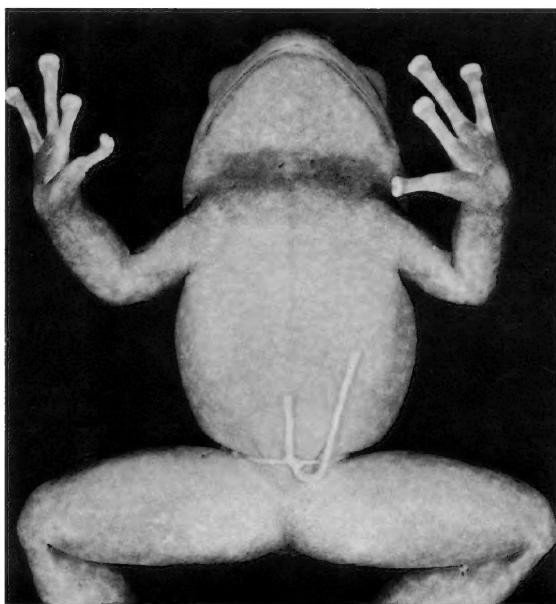


Fig. 4. An adult male *Aromobates nocturnus* (EBRG 2220) showing maximum development of the gray throat collar,  $\times 1.25$ . This marking is usually fainter (e.g., see fig. 18A).

the hands and feet are brown except toward the end of the digits and on the foot webbing, which are unpigmented.

#### MYOLOGY

Freshly skinned frogs have light gray flesh, sometimes with patches of white on the thighs, where melanophores are absent or particularly sparse. The dorsal musculature remains pale gray on preserved carcasses, but melanophores elsewhere are so sparsely or patchily distributed that the flesh is whitish. Jaw and thigh muscles are similar to the usual condition among dendrobatids, except for the presence in some specimens of an additional jaw muscle. A few muscle states of known taxonomic usefulness were coded from 11 skinned paratopotypes, most of which were subsequently cleared-and-stained for bone and cartilage.

The m. adductor mandibulae externus superficialis is present in most individuals (fig. 5); although varying somewhat in thickness, this muscle is present on at least one side in 9 of 11 specimens dissected (present on both sides in 6 individuals, one side only in 3). The deeper m. adductor mandibulae poste-

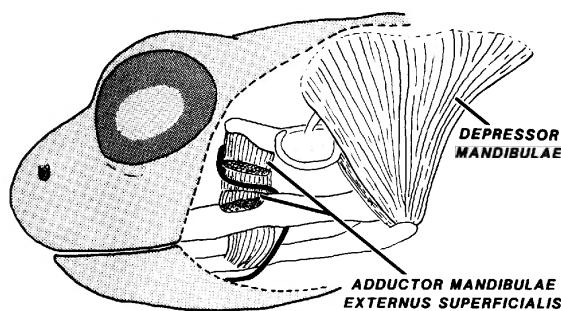


Fig. 5. Head of *Aromobates nocturnus*, showing certain jaw muscles: The m. adductor mandibulae externus superficialis is cut and deflected to show path of underlying nerve (mandibular branch of trigeminal nerve); this is the first report of the superficial external adductor in the Dendrobatidae, whereas the muscle mediad to the nerve—the adductor mandibulae posterior subexternus—is always present. The concealment of the posterodorsal edge of the tympanum, by the anterior edge of the large superficial slip of the m. depressor mandibulae, is a dendrobatid synapomorphy.

rior subexternus is present in all. Both muscles originate from the zygomatic ramus of the squamosal, with the mandibular branch of the trigeminal nerve lying between them.

A massive superficial slip of the m. depressor mandibulae originates from the dorsal fascia and conceals all but the anteroventral part of a smaller, deeper slip (visible in fig. 5). The latter originates dorsally from the proximal part of the otic ramus of the squamosal and anteriorly from along the posterior margin of the tympanic ring. The large superficial slip of the depressor mandibulae very slightly overlaps the posterodorsal margin of the tympanic ring (fig. 5).

On the thigh, the distal tendon of the deep m. semitendinosus pierces the distal tendinous end of the m. gracilis complex prior to insertion (fig. 6B). The tendinous inscription across the middle of the gracilis major muscle is barely indented but clearly indicated (fig. 6A); the concealed dorsal wall of the gracilis major has a well-defined concavity that is occupied by the two heads of the semitendinosus muscle (fig. 6B).

The m. gracilis minor originates by its own tendon from the pelvic rim and extends as a narrow, very thin muscle along the dorsal edge of the m. gracilis major along the posterior face of the thigh. The fibers are inter-

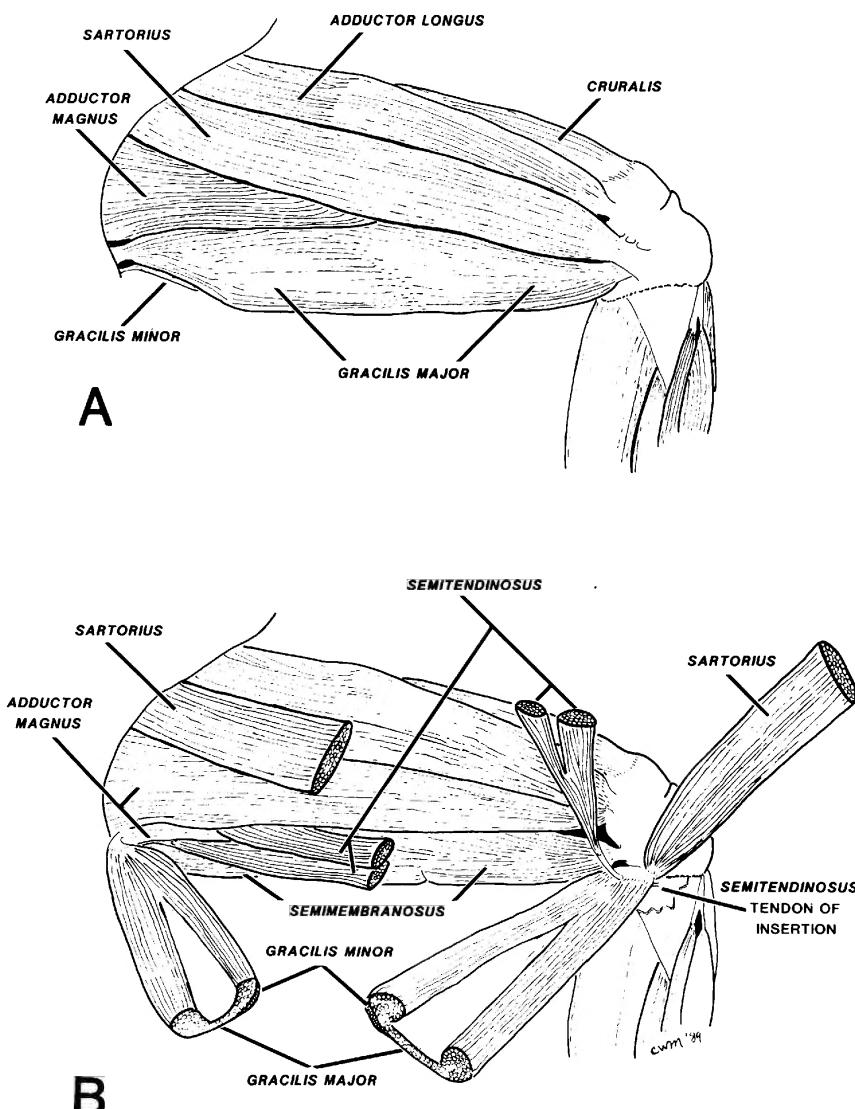


Fig. 6. Ventral view of left thigh of *Aromobates nocturnus* (AMNH 130034). A. Superficial muscles. B. The m. sartorius, m. gracilis, and the deeper m. semitendinosus are cut and reflected, to show route of semitendinosus tendon through the distal end of the gracilis complex.

rupted by a short interval of tendon at a distance of about 15 percent the length of the gracilis minor from its point of origin. It remains distinct but closely appressed to the gracilis major for its entire length, although sharing a common tendinous insertion with the latter.

#### OSTEOLOGY

The following description is based on six dry skeletons and eight cleared-and-stained specimens (2 stained for bones only, 6 dou-

ble-stained for bones and cartilage). All are paratopotypes.

**SKULL:** Skull (fig. 7) much wider than long. Frontoparietals heavily ossified and in generally close contact, sometimes with a slight anteromedial divergence and sometimes posteriorly fused. Sphenethmoid large, with a concavity at anteromedial margin and overlapped by the frontoparietals posteriorly. Moderate size nasal bones widely separated, overlapping the anterolateral margins of the sphenethmoid; elongated maxillary process

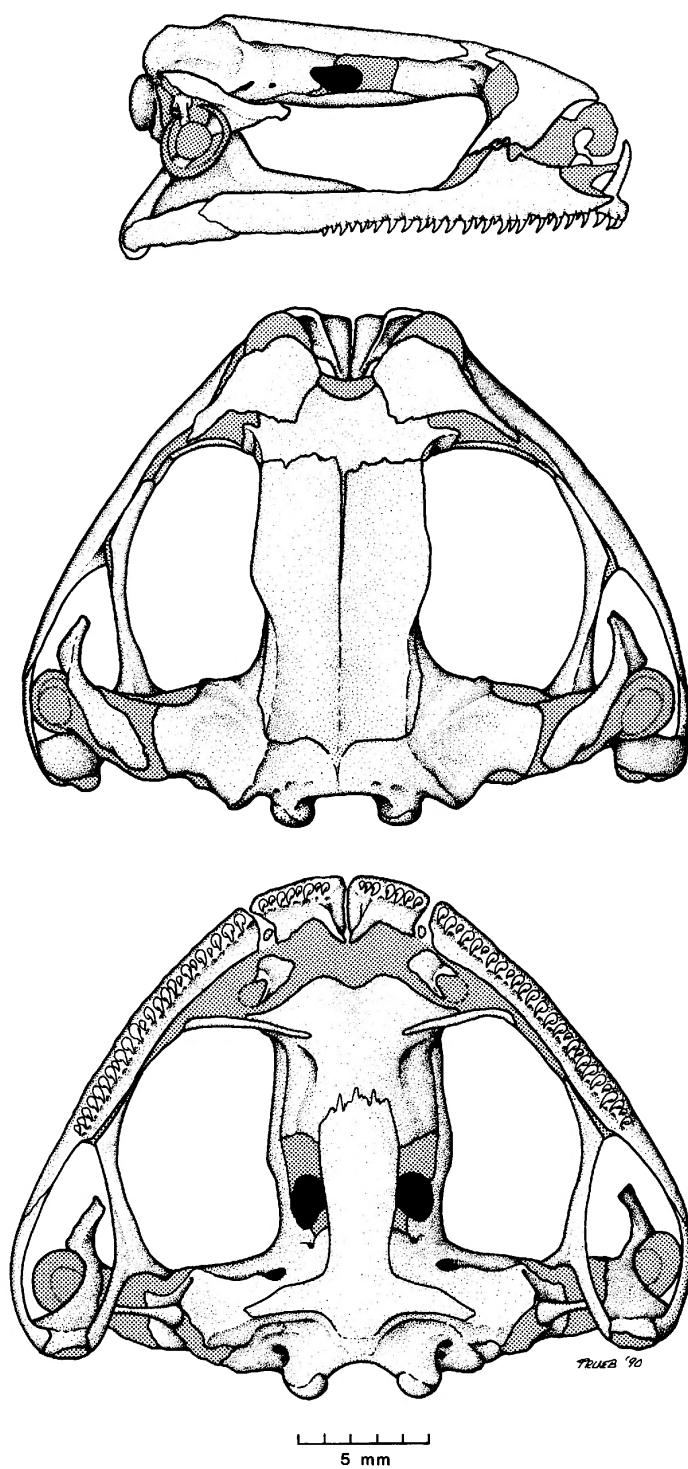


Fig. 7. Skull of *Aromobates nocturnus* (AMNH 130040), in lateral, dorsal, and ventral views. Cartilage gray. Soft tissue of anterior palate as well as cartilaginous region also gray in bottom drawing; limits of choanae shown by broken line.

of nasal reaching level of (and sometimes overlapping) facial lobe of maxilla.

Ventrolateral processes of sphenethmoid<sup>7</sup> short, possibly serving as braces for long narrow palatine bones. Vomers toothless and widely separated, somewhat variable in shape, supporting medial margins of choanae. Small septomaxillae lie anterior to lower anterior edges of vomers. Sphenethmoid fused mid-ventrally, ventrolaterally separated from optic foramen by cartilage. Anterior end of cultriform process of parasphenoid overlapping posterior part of sphenethmoid in midorbital area; anterior edge of cultriform process ragged or serrate; sides nearly parallel; parasphenoid alae posterolaterally oriented, moderately short; posteromedial parasphenoid may be fused to exoccipitals dorsally. Posterior braincase complete, with paired exoccipitals and prootics fused to contralateral member and one another. Lateral and posterolateral otic capsule cartilaginous; distal half of crista parotica cartilaginous. Pars media plectri long, well developed, and distally associated with subcircular plate of cartilage—pars externa plectri. Latter located within tympanic annulus, which is incomplete posterodorsally (11:00 o'clock).

Alary processes of premaxillae massive, projected slightly anterodorsally and also tilted slightly laterally. Nonpedicellate,<sup>8</sup> inwardly curved, fanglike teeth on premaxillae and maxillae, the maxillary teeth decreasing in size posteriorly. Pars facialis of maxilla moderately deep and well ossified, with an irregularly shaped dorsal preorbital process great-

<sup>7</sup> According to Trueb (1973: 82), this process represents ossification of the cartilaginous planum antorbitale. In some dendrobatiids lacking palatine bones, the process is elongated and extends close to the pars facialis of the maxilla.

<sup>8</sup> That is, the teeth show no evident line of division between a crown and pedicel, nor is there any pattern of physical separation of crowns from pedicels (breakage is irregular). The loss or significant obfuscation of the usual amphibian pedicellate condition warrants attention as a possible additional synapomorphy for the Dendrobatiidae. Parsons and Williams (1962: 377) were unable to find evidence of pedicellate teeth in two dendrobatiids examined and Myers has not noticed the condition during examination of various cleared-and-stained dendrobatiids, but histological evidence would be welcome.

ly increasing its height; pars facialis with a steeply inclined posterior margin from top of preorbital process to maxilla; anterior end of maxilla in close contact with but not overlapping premaxilla, posterior end broadly articulating with quadratojugal. Squamosal markedly triradiate, with pronounced anteriorly projected zygomatic ramus (curved anteromedially), a long otic ramus braced against and overlapping edge of the crista parotica, and a longer ventral ramus in contact with the quadratojugal and pterygoid; relative length of squamosal branches: ventral ramus > otic ramus > zygomatic ramus. Anterior and posterior rami of pterygoid robust; shorter medial process of pterygoid present, closely approaching or in contact with ventrolateral edge of otic capsule (prootic). Retroarticular process of mandible present, but always short (compared with dendrobatiids generally) although somewhat variable in length.

**HYOLARYNGEAL SKELETON:** Hyoid plate (fig. 8) cartilaginous, wider than long. Each hyale bearing a single, short slender anterior process curving anterolaterally. Alary processes distally expanded and directed anterolaterally; posterolateral processes slender; posteromedial processes ossified except for distal cartilaginous tips. Cricoid ring complete (dorsally or ventrally broken in some preparations). Paired arytenoid cartilages well separated.

**VERTEBRAE:** Eight procoelous vertebrae, with nonimbricate neural arches. No vertebral fusions except for a joining of cervical and second vertebra on ventral side in one adult female (AMNH 130047). Transverse processes of vertebra II relatively short, of vertebrae III relatively long, of vertebrae IV–VIII subequal but nearly as long as on vertebrae III. Sacral processes dilated distally (fig. 9). Sacral-coccygeal articulation bicondylar.

**PECTORAL GIRDLE:** Firmisternal (i.e., coracoids firmly united by undivided epicoracoid cartilage<sup>9</sup>). Coracoids much wider than long, greatly expanded along medial contact

<sup>9</sup> Also firmisternal in the sense of Ford (MS: 226), who treats firmisterny as a complex character.

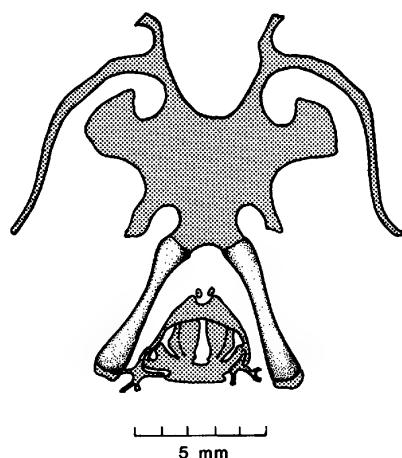


Fig. 8. Hyoid apparatus of *Aromobates nocturnus* (AMNH 130040). Cartilage gray.

(fig. 10). Clavicles long and slender, laterally fused with scapulae and very nearly abutting medially near anteroventral margins of coracoids. Procoracoid cartilages coextensive with clavicles, each procoracoid fitting in a trough in the posterodorsal surface of a clavicle. Epicoracoid cartilages fused with each other (at least posteriorly) between coracoids and with procoracoids. Sternum completely cartilaginous and variably shaped. Omosternum present as a terminally bifurcate structure, cartilaginous, usually with a small proximal center of calcification. Suprascapulae ossified on lateral halves and across anterior margins; cleithra simple (nonbifurcate) bones fused against anterior margins of suprascapulae, laterally reaching scapulae.

**PHALANGES:** Phalangeal formula of hands 2-2-3-3, of feet 2-2-3-4-3. Each terminal phalanx prominently T-shaped, with the transverse process positioned approximately across the middle of the fleshy digital disc; transverse process wider than the length of its stem and more than twice as wide as penultimate phalanx at midpoint.

#### TADPOLES

**IDENTIFICATION:** Two kinds of dendrobatid tadpoles were found in the same streams occupied by adult *Aromobates nocturnus*: Tadpoles belonging to a sympatric species of *Colostethus* were quite abundant and easily caught with a small net; these attain a max-



Fig. 9. Dilated sacral diapophyses of *Aromobates nocturnus* (AMNH 130048),  $\times 5.8$ .

imum total length of about 40 mm in stages 32-34, with identification being confirmed by one metamorphosing individual. Compared with two tadpoles assigned to *Aromobates* (see below), 45 *Colostethus* tadpoles (stages 25-34) have stouter bodies (midbody width 55-67% of head-body length vs. 52-55% in *Aromobates*), shorter tails (tail length 53-60% of total length vs. 61-64%), and deeper tail fins (greatest tail depth 19-32% of total length vs. 16-19%). The *Colostethus* larvae also have more strongly serrated beaks, translucent venters and paler tails, with melanophores on the caudal surfaces being more conspicuously clumped than in larger and darker larvae assigned to *Aromobates*.

A large ( $> 60$  mm total length), relatively uncommon and harder-to-catch black tadpole undoubtedly belongs to *Aromobates nocturnus*; two individuals with hind limbs showing stages in toe development were collected and are described below.

**MEASUREMENTS** (in mm): One large larva in Gosner stage 34 (AMNH 130051) and a slightly smaller one in stage 37 (AMNH 130050) have the following measurements, respectively: Total length 68.1, 65.5; head-body length 26.3, 23.3; midbody width 14.5, 12.2; midbody depth 12.4, 10.4; greatest tail depth from upper edge of dorsal fin to lower edge of ventral fin 12.9, 10.5; width of oral disc 8.6, 7.5.

**HABITUS AND PROPORTIONS:** Viewed from above, the head and body form an elongated ellipse rounded at both ends and as wide (or a little wider) anteriorly as posteriorly (fig.

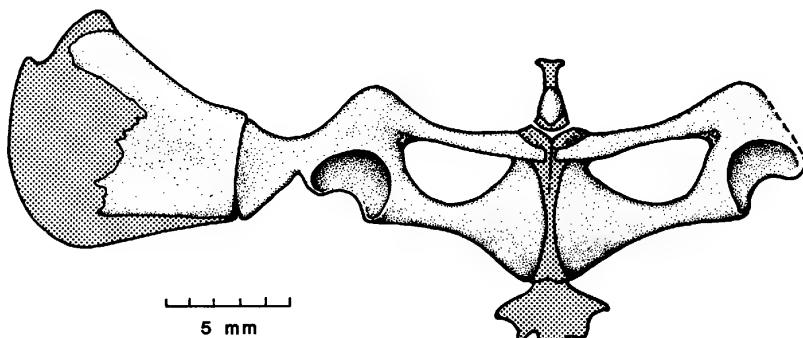


Fig. 10. Pectoral girdle of *Aromobates nocturnus* (AMNH 130040), in ventral view. Lateral components deflected to ventral plane; left suprascapula not shown. Cartilage gray.

11), with midbody width 52.4–55.1 percent of head-body length. The head and body are depressed (midbody depth = 85.2–85.5% of midbody width), slightly flattened dorsally and ventrally. Eyes and nostrils in a dorsal position, with nares directed anterodorsally

and the eyes with a more dorsolateral orientation. The spiracle is sinistral and the anus dextral. The low-finned tail is 61–64 percent of total length and its greatest depth is 16–19 percent of total length. The dorsal fin becomes slightly thickened anteriorly as it

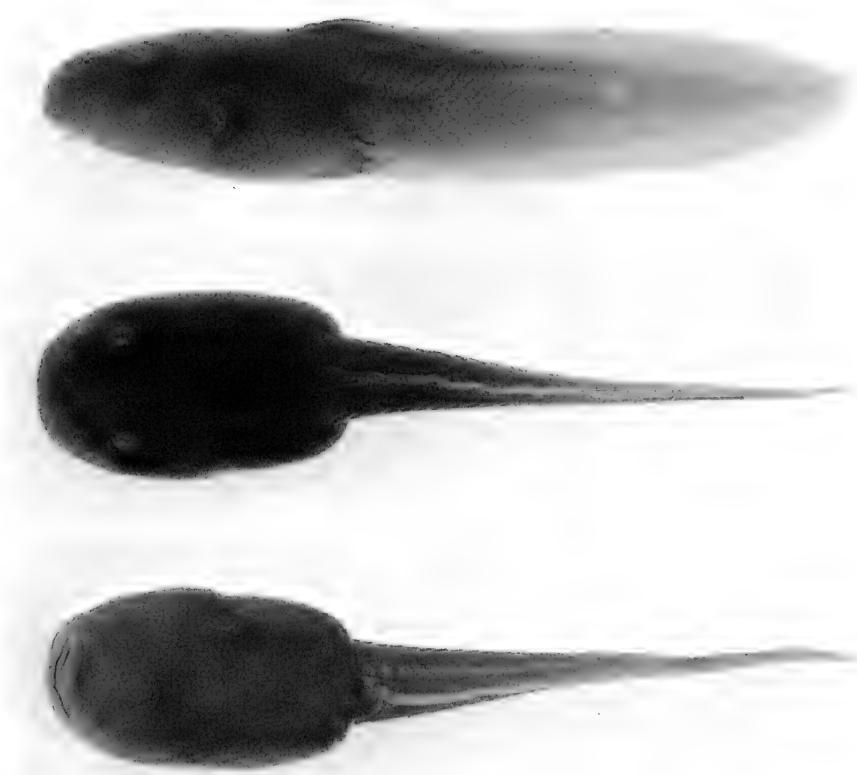


Fig. 11. Tadpole of *Aromobates nocturnus* (AMNH 130051, stage 34),  $\times 1.5$ .

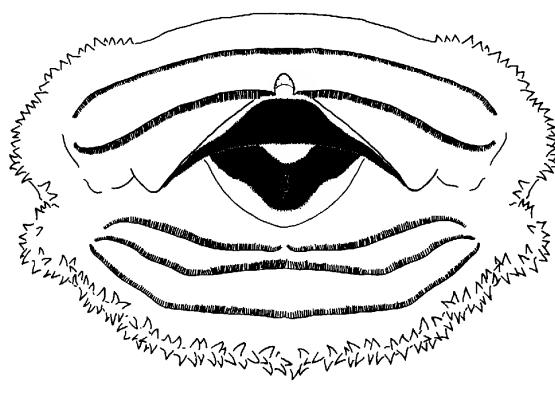


Fig. 12. Mouth of *Aromobates nocturnus* tadpole (AMNH 130050, stage 37). Line equals 1 mm.

reaches the body; the end of the tail is rounded.

**PIGMENTATION:** These large tadpoles appeared overall black in life. In preservative, the head and body are uniformly dark gray-brown dorsally, gradually turning medium gray on the opaque (internal organs not clearly visible) venter. Caudal musculature light brown, with melanophores sparsely but rather uniformly distributed. Dorsal and ventral fins gray with vague brown blotching, which is most pronounced on the darker dorsal fin.

**MOUTH PARTS:** The mouth (fig. 12) is directed anteroventrally. The tooth-row formula is 2/3, with the second upper row distinctly notched and broken above the beak and the first lower row very narrowly broken below the beak. The beak is massively ( $>1/2$ ) keratinized but its width occupies only about the median one-third of the oral disc; the upper and lower cutting edges are very finely serrated. The upper beak is flattened across the major part of its keratinized face; the lower beak is weakly V-shaped. The oral disc is laterally indented. The median anterior edge of the oral disc is nude, but its anterolateral, lateral, and posterior edges are continuously fringed with short, pointed papillae, which change from a single row anteriorly to a double row posteriorly.

#### BIOCHEMISTRY OF SKIN SECRETIONS

Ten adult females were skinned in the field and the skins stored in 100 percent methanol, for the following analyses.

**TEST FOR TOXICITY:** Subcutaneous injection of methanol extract equivalent to 0.2 g wet weight of skin had no apparent effect on 20-g white mice, nor did an injection of an equivalent amount of aqueous extract.

**ASSAY FOR SKIN ALKALOIDS:** Following well-tested protocol (Daly et al., 1987: 1024–1026), methanol skin extracts were fractionated to yield an “alkaloid fraction.” As assessed by thin-layer chromatography, gas chromatography–mass spectrometry, and thermospray mass spectrometry, this fraction contained no alkaloids.

The mass spectrometric techniques are very sensitive, particularly for alkaloids, so it seems unlikely that skin of *Aromobates nocturnus* contains even trace amounts of alkaloids.

**THE VOLATILE SECRETION:** The unpleasant odor of *Aromobates nocturnus* is distinctively noxious (see Chemical Defense under Distribution and Natural History) and was captured in the methanol extracts. But to this time it has defied analysis.

Efforts to demonstrate mercaptans or other volatile compounds that might account for the odor have been unsuccessful. Air was passed over a live frog or nitrogen was bubbled through odoriferous methanolic skin extracts. The volatile compounds in the effluent air or in the nitrogen were then collected either in a small volume of methanol at liquid N<sub>2</sub> temperature or in a Carbotrap 100 thermal desorption tube (Supelco Inc., Bellefonte, Penn.). Gas chromatographic–mass spectral analyses of material trapped in the methanol and of adsorbed material released on heating of desorption tubes failed to detect any volatile substance that might account for the odor.

It should be noted that the human olfactory system is extremely sensitive, being able in some cases to detect mercaptans at the parts per billion level. This fact plus the negative analytical results suggest that the volatile compound responsible for the odor probably is present at a much lower level than is subjectively suggested by the odor itself.

#### DISTRIBUTION AND NATURAL HISTORY

**DISTRIBUTION:** *Aromobates nocturnus* occurs near the extreme northern terminus of the Venezuelan Andes, at an elevation ( $\approx$



Fig. 13. Andean cloud forest at 2300 m above sea level, roughly 2 km airline ESE Agua de Obispos on road to La Peña, above type locality (downhill from foreground in these scenes) of *Aromobates nocturnus*; photographed November 30, 1987.

2250 m) that was probably only about 700–1300 m below the lowest limits of Pleistocene glaciation farther south in this sierra (Salgado-Labouriau, 1984; Schubert, 1984). The Venezuelan Andes (including the Mérida An-

des), which branch off from the Cordillera Oriental at the Colombian boundary, are bordered to the west by the Maracaibo Basin and to the east by the great expanse of Llanos of the western Orinoco drainage. Foothills to

the north (a series of low and rather dry sierras) continue nearly to the Atlantic coast. To the northeast, the dry Yaracuy-Barquisimeto Depression sets off the Andean foothills from the Cordillera de la Costa—a sub-Andean range that extends brokenly across the north coast of Venezuela to Trinidad.

Physiographic considerations therefore suggest that *Aromobates nocturnus* is likely to have either a very small geographic range or else a larger, disjunct distribution that might extend southeastward from the type locality, which lies in an apparently isolated tract of cloud forest. (A third possibility, that *A. nocturnus* might also occur in suitable habitat in higher (> 2000 m) sections of the Cordillera de la Costa, is at least conceivable.)

**HABITAT:** The type locality lies in a dense cloud forest (fig. 13) that is isolated by lower, more open country on at least the eastern, northern, and western sides (southern side not examined). This subpáramo habitat may be the highest vegetational zone in the immediate region, although isolated páramos (above 3000 m) occur both to the north and south.

*Aromobates nocturnus* was most abundant in rivulets and spring runs  $\leq 0.5$  m wide, with a depth ranging from a few cm to about 0.5 m; water temperature was 12.4°C. It was virtually impossible to work along these headwater streamlets in undisturbed cloud forest, so dense was the vegetation, and we collected mostly in forest-edge situations along an unpaved road. Here, in relatively open situations, the rivulets were densely edged with grasses and ferns (fig. 14). The frog was decidedly less common downslope in a canopy-covered stream  $\geq 1$  m wide; this larger stream had faster water, small boulders, and lacked an edge growth of grasses and ferns.

**BEHAVIOR:** This species appears to be completely nocturnal. They were to be found sitting out in the open from shortly after dark to at least midnight, on each of three collecting nights (November 28–30, 1987), consistent with Paolillo's original observations in December 1981. There was moonlight during parts of the first two nights, but the night of November 30 was dark owing to heavy cloud cover. They were not seen in the open by day, but several frogs were flushed from concealment in thick grass in water at

stream-edge, and one was pulled from under a small rock ledge at the edge of a rivulet.

*Aromobates nocturnus* is decidedly aquatic in contrast to other dendrobatids. Not one was found away from a stream, and only a few were sitting slightly out of water. All others were found sitting in shallow water or were seen swimming under water. They have a serene disposition and are usually easily caught, but if the collector is clumsy they will dive and hide under water but soon return to their original location. Limited observation on successive nights indicated that individual frogs stay close to one spot; no aggression was seen in a few instances when one frog moved close to another. They readily ate insects thrown to them in the illumination of a headlight; one left its stream in one or two strides to catch a proffered crane fly and then returned to water. When not swimming, they seem to prefer to walk rather than to jump or leap.

*Aromobates* was not heard to call, and we have no information on reproductive behavior.

**CHEMICAL DEFENSE:** The skin of stressed *Aromobates* was not particularly distasteful to us and certainly lacked the bitter taste produced by many dendrobatid skin alkaloids. But our frogs invariably gave off a vile mercaptanlike odor when they were caught and they also produced a sticky mucus. The offensive odor was produced only upon handling (frogs kept in closed containers were odorless until seized) and clearly seems to have a defensive function. *Aromobates nocturnus* therefore has noxious properties but is not toxic (see preceding section, Biochemistry of Skin Secretions). In the mouths of some predators, the secreted mucus may be sufficiently sticky to provide some mechanical defense as in the case of certain other amphibians (see Daly et al., 1987: 1066).

#### FAMILIAL PLACEMENT AND COMPARISONS

*Aromobates nocturnus* is assigned to the family Dendrobatidae on the basis of a suite of derived characters, including, but not limited to, the following: (1) paired digital scutes; (2) tympanum posterodorsally tilted under anterior edge of the massive superficial slip of the *m. depressor mandibulae*; (3) insertion



Fig. 14. Small-stream habitats in roadside clearing through dense cloud forest (November 30, 1987). *Aromobates nocturnus* seems highly aquatic in these shallow rivulets, swimming and sitting in the water by night, and concealing itself by day in aquatic vegetation or streamside crevices.

tendon of the m. semitendinosus piercing that of the mm. gracilis complex; (4) alary processes of premaxillae projected anterodorsally; (5) firmisternal pectoral girdle with pro-

coracoid cartilages slender and coextensive with clavicles that nearly meet at midline; and (6) T-shaped terminal phalanges. The second character seems to be unique to the

Dendrobatidae (Myers and Daly, 1979: 8; Myers and Ford, 1986: 10), the fourth character nearly so (Ford, MS), and the others serve in combination to diagnose the family.

A suite of primitive character states, including absence of skin alkaloids, absence of aposematic coloration, presence of palatine bones, and a pronounced outwardly sloping (not weakly sloping to vertical) loreal region, precludes *Aromobates* from the lipophilic alkaloid-producing group presently comprising the genera *Epipedobates* (including *Allobates* and *Phobobates*<sup>10</sup>), *Minyobates*, *Phyllobates*, and *Dendrobates* (Myers, 1987).

The remaining dendrobatid genus currently recognized is *Colostethus*, a large assemblage of usually small and cryptically colored brown frogs whose phylogenetic relationships are unresolved (although phenetic groupings were provided by Edwards, 1974). A monophyletic subset of this taxonomically vague group is definable by a unique synapomorphy, however, and can be excluded from close consideration with *Aromobates*.

#### TOWARD A DEFINITION OF *COLOSTETHUS* COPE (1866)

Including a few undescribed species, a dozen or so small (roughly 20–35 mm SVL) dendrobatids are characterized by presence of a

<sup>10</sup> Along with Schulte (1989), we cannot justify recognizing either of these recently described genera at this time: The monotypic *Allobates* Zimmermann and Zimmermann (1988) especially seems to add to problems of paraphyly at the basal part of the lipophilic alkaloid-producing group, since apparently close relatives (Pyburn, 1981) of the type species were left in *Epipedobates*. *Phobobates* Zimmermann and Zimmermann (1988) was erected for the three members of the *E. trivittatus* species group, whose monophyly is supported by the “retarded trill call”—defined and described by Myers and Daly (1979: 18) for two of the species and subsequently recorded by Schulte (1981) for the third. In proposing a new genus for this species group, Zimmermann and Zimmermann claimed an additional, potentially persuasive, synapomorphy, namely absence of amplexus in mating (based on terrarium studies). However, field observations by Schulte (1981) on *E. bassleri* and by Henzl (MS.) on *E. trivittatus* show that cephalic amplexus does occur in the group—as predicted by Myers (1987) for all species placed in the plesiomorphic genus *Epipedobates*. Elevating the *trivittatus* species group to generic status does not elucidate relationships in any new way.

widened or swollen third finger in adult males. This curious feature is present in *Colostethus* but unknown elsewhere in the Dendrobatidae. Nearly all recent workers on *Colostethus* taxonomy have used or have mentioned the character, but no one seems to have recognized its uniqueness within the family or investigated its intraspecific variation. It characterizes the type species both of *Colostethus* (type species = *Phyllobates latinus* Cope, by original designation) and the junior synonym *Prostherapis* (type species = *P. inguinalis* Cope, by monotypy). The senior author is familiar with both species based on fieldwork in Panama; they represent ecological extremes in the genus: *C. latinus* is a webless, terrestrial frog of montane rain forest (> 1000 m elev.), whereas *C. inguinalis* is a webbed, riparian species of lowland and lower montane rain forest (≤ 800 m elev.). Such extremes in morphology and behavior have contributed to making this a taxonomically “difficult” group. It is sometimes useful in such cases to set aside any named assemblage that can be defined by novel synapomorphy, even though such clades may become subsumed with accumulation of more comprehensive information.

A restricted *Colostethus* can be resolved by the novel third-finger synapomorphy, although use of this sexually dimorphic character is not without problems. The character is expressed more strongly in some species than in others and, in some species at least, it is not expressed in all adult males in a given sample. The intraspecific variability and a probable function in cephalic amplexus suggest that the character is under hormonal control.

**CONTENT:** The following named species are known to have the defining synapomorphy: *Colostethus agilis*\* Lynch and Ruiz-Carranza, 1985 (inclusion based on original description); *Colostethus brachistriatus*\* Rivero and Serna, 1986 (inclusion based on subsequent description of males by Rivero and Serna, “1988” [1989]: 145); *Phyllobates flotator* Dunn, 1931; *Colostethus fraterdanieli* Silverstone, 1971; *Colostethus imbriculus* Silverstone, 1975; *Prostherapis inguinalis* Cope, 1868; *Phyllobates latinus* Cope, 1863; *Phyllobates mertensi*\* Cochran and Goin, 1964 (inclusion based on Edwards, 1974);

*Phyllobates nubicola* Dunn, 1924; *Phyllobates pratti* Boulenger, 1899; *Colostethus stepheni*\* Martins, 1989.

An asterisk (\*) following a name indicates species not examined but included on the basis of a published description of the dilated third finger in adult males. Species for which the character description is ambiguous are excluded (e.g., Rivero and Granados Díaz, "1989" [1990]).

**DISTRIBUTION:** Mainly lower Central America and northwestern South America, but with some representation east of the Andes, including the recently named *C. stepheni* from Amazonia (Martins, 1989) and another one to be described from the Guayana region (Myers and Arnold, in progress).

**REMARKS:** *Colostethus inguinalis* is the only member of this genus or of "Hyloxalus" (see below) so far demonstrated to have a skin toxin, although it is a water-soluble compound still of unknown structure—possibly an alkaloid but not a lipophilic alkaloid such as characterizes other toxic dendrobatiids (Neuwirth et al., 1979; Daly et al., 1987). The closest relative of *C. inguinalis* may be *C. imbriculus*. Neither water-soluble toxins nor lipophilic alkaloids could be demonstrated in a single skin (0.2 g) of *imbriculus* obtained by Daly and Myers at the type locality in 1978 (although very marginal effects were noted in mouse assay). But *imbriculus* shares with most individuals of *inguinalis* the unusual feature of having a full set of golden yellow to orange flash marks (i.e., axillary, inguinal, and calf spots all present in life); these are both webbed-toed riparian lowland species.

#### ON THE NAME *HYLOXALUS* JIMÉNEZ DE LA ESPADA (1871)

If *Colostethus* is used in the restricted sense above, the name *Hyloxalus* becomes available for the residual species. *Hyloxalus* was erected by Jiménez de la Espada (1871: 59) for two new species, *H. fuliginosus* and *H. bocagei*, which were figured in a subsequent work (Jiménez de la Espada, 1875: pl. 1, figs. 1, 2). The type species is *Hyloxalus fuliginosus* by subsequent designation (Savage, 1968: 747). The junior synonym *Hylixalus* Boulenger (1882: 137–138) is, by current standards of nomenclature, an "unjustified"

emendation of *Hyloxalus* that automatically takes the same type species. Another available but later name than *Hyloxalus* is *Phyllodromus* Jiménez de la Espada (1875, pl. 3, fig. 3 [by indication, no description]), which has as type species *Phyllodromus pulchellum* Jiménez de la Espada (loc. cit.) by monotypy.

*Colostethus* is overdue for partitioning and we find it useful (e.g., in fig. 20) to start considering a resurrected *Hyloxalus*. But we have yet to examine specimens on which the type species is based and are not at this time attempting to formalize a major nomenclatural change. In the present paper we continue using the name *Colostethus* broadly, with the added conventions "sensu stricto" (s.s.) or "sensu lato" (s.l.) as needed. We shall occasionally use the admittedly awkward phrasing "*Colostethus* s.l. (*Hyloxalus*)" when we wish explicitly to exclude *Colostethus* s.s.

Meanwhile, *Aromobates* is readily distinguished from *Colostethus* s.s. by much larger size and absence of a swollen third finger in males. *Colostethus* s.s. appears not to occur in the greater part of Venezuela.

#### COMPARISONS WITH "COLLARED *COLOSTETHUS*"

A few dozen named *Colostethus* s. l. (*Hyloxalus*) are known from Venezuela (table 2), and it is a subset of those that may be phylogenetically closest to *Aromobates*: certain Venezuelan species, and one each from Trinidad and Tobago, share with *Aromobates nocturnus* the unusual feature of a dark gray to black collar lying transversely across the base of the throat (table 2).<sup>11</sup> Such a color pattern in the Dendrobatiidae has not previously been found outside of *Colostethus*. The presence of a throat collar is nearly confined to Venezuelan frogs—although a similar marking is shared by at least one Andean species (fig. 15A). It is tempting to consider

<sup>11</sup> This marking, which occurs just anterior to the pectoral girdle and arm insertions, is variously referred to in the literature as a "pectoral collar," "collar pectoral," "collar en el pecho," "transverse chest band," or "chest bar." It can hardly be homologous with dark markings—properly called chest or pectoral spots—that are positioned between the arm insertions in some *Colostethus* (e.g., see Edwards, 1974: 21, fig. 4A). For this reason we prefer "throat collar" or "throat bar" as descriptive terms.

TABLE 2  
Distribution of Selected Characters in *Colostethus* s.l. (*Hyloxalus*) from  
Venezuela, Trinidad, and Tobago

Species	Toe webbing		Dorsal-lateral stripe	Lateral oblique stripe		Throat collar	Source <sup>a</sup>
	Extensive	Basal		Complete	Incomplete		
<i>C. alboguttatus</i>	—	+	+	—	—	—	1, 2, 3
<i>C. bromelicola</i>	—	?	+	—	—	—	1, 3
<i>C. collaris</i>	—	+	—	—	+	+	1, 2, 3
<i>C. dunnii</i>	+	—	—	—	+	—	1, 3
<i>C. duranti</i>	—	+	+	—	—	—	1
<i>C. guatopoensis</i>	+	—	—	—	—	+	1
<i>C. haydeae</i>	—	+	+	—	—	—	1
<i>C. herminiae</i>	—	+	±	—	+	+	1, 2, 3
<i>C. humilis</i>	—	+	—	?	—	—	1
<i>C. inflexus</i>	—	+	—	+	—	—	1
<i>C. leopardalis</i>	—	+	+	—	+	±	1
<i>C. mandelorum</i>	—	+	+	—	+	—	1, 3
<i>C. mayorgai</i>	—	+	—	+	—	—	1
<i>C. meridensis</i>	—	+	—	—	—	—	[1], 3
<i>C. molinarii</i>	—	+	+	—	—	—	1
<i>C. neblina</i>	—	+	+	—	+	+	1, 2
<i>C. obliteratus</i>	+	—	—	—	+	+	1
<i>C. olmonae</i>	—	+	±	—	+	+	1, 2, 3
<i>C. orostoma</i>	—	+	+	—	—	—	1
<i>C. riveroi</i>	—	+	±	—	+	+	1, [2], 3
<i>C. saltuensis</i>	—	+	+	—	+	—	1
<i>C. sanmartini</i>	—	+	+	—	+	±?	1
<i>C. serranus</i>	—	+	+	—	—	—	1
<i>C. shrevei</i>	+	—	—	—	+	—	1, 2
<i>C. trinitatis</i>	—	+	±	—	+	+	1, 2, 3
<i>C. yustizi</i>	—	+	+	—	+	+	1
<i>C. new species</i>	—	+	—	—	+	+	1 = 3

<sup>a</sup> Source of data: 1 = original description; 2 = personal examination; 3 = Edwards, 1974. Brackets [ ] indicate data source used in case of substantial disagreement. For nomenclatural citations to species not in Frost (1985: 87–96), see: Dixon and Rivero-Blanco, 1985 (*guatopoensis*); La Marca, 1985, 1989 (*molinarii* and *yustizi*); Péfaut, 1985 (*duranti* and *serranus*); Rivero, 1984 (*oblitteratus*); Rivero et al., 1986 (*sanmartini*). Formally undescribed Venezuelan species are excluded from this table except for one considered by Edwards (1974: 272–276).

as a synapomorphy any distinctive and geographically restricted character such as the throat collar unless there is reason to suspect symplesiomorphy or homoplasy. Judged from a rather confused literature, there are indeed problems in determining homology based on collarlike markings alone, even if species from western South America are excluded as in the following discussion. As shown in table 2, we are aware of 10 seemingly unequivocally collared species of *Colostethus* being mentioned in the literature and two others (*leopardalis* and *sanmartini*, neither seen by us) for which some doubt exists as to the nature or presence of a bona fide collar. Of these 12 species, one

each is confined to Trinidad or Tobago and 10 are Venezuela endemics, as follow:

1. *C. collaris* (Boulenger)—Venezuelan Andes.
2. *C. guatopoensis*<sup>12</sup> Dixon and Rivero-Blanco—North-central Venezuela, Serranía del Interior.
3. *C. herminiae* (Boettger)—Northern Venezuela in Cordillera de la Costa and Serranía del Interior (possibly a composite of sibling species).

<sup>12</sup> It seems likely that *Colostethus guatopoensis* Dixon and Rivero-Blanco (1985) is conspecific with *C. obliteratus* Rivero (1984). But we have not seen material and treat both as valid for present purposes.

4. *C. leopardalis* Rivero—Venezuelan Andes.
5. *C. neblina* (Test)—North-central Venezuela in Cordillera de la Costa.
6. *C. obliteratus* Rivero—North-central Venezuela, Serranía del Interior.
7. *C. olmonae* Hardy—Tobago Island.
8. *C. riveroi* (Donoso-Barros)—NE Venezuela, >600 m in Paria Peninsula.
9. *C. sanmartini* Rivero, Langone, and Prigioni—NE Venezuela, lower Río Orinoco.
10. *C. trinitatis* (Boulenger)—Trinidad.
11. *C. yustizi* La Marca—Venezuelan Andes (Serranía de Portuguesa).
12. Unnamed species (described in Edwards, 1974: 272–276)—NE Venezuela, >600 m in Paria Peninsula. An additional unnamed collared species may be isolated in the western Venezuelan llanos according to Péfaur (1987). See also Figure 15B.

Although Edwards (1974) did not attempt to assign phylogenetic significance to the throat collar,<sup>13</sup> Rivero (1979: 169) suggested that the characteristic collar “es evidencia de mucho peso a favor de que las especies acollaradas constituyen un grupo filogenético afin.” However, Rivero (1984: 54) later cited Haydée Laukeninks’ unpublished morphometric and biochemical data on Venezuelan Andean *Colostethus*; Rivero said that these data suggested that the collared *collaris* and the sometimes collared *leopardalis* are each more closely related with noncollared species (*meridensis* and *alboguttatus*, respectively) than with each other. A close relationship between *leopardalis* and the noncollared *alboguttatus* was originally suggested in Rivero’s (“1976” [1978]) description of *leopardalis*, which was said to have “un leve collar oscuro casi siempre presente en la garganta.” Such a relationship also was accepted by La Marca (1985: 4), who claimed that an *alboguttatus* species group is a monophyletic as-

semblage of eight species including *leopardalis* (the only one in the group having been described as sometimes collared). La Marca (1989) more recently included eight named species in a *collaris* species group, without reference to *leopardalis*, *sanmartini*, or *oblitteratus*—the last species having been explicitly described as having “un collar bien definido” (Rivero, 1984: 53).

If a collar or traces of one do appear in the variation of *leopardalis* and if Rivero’s and La Marca’s placement of this species in a noncollared group proves correct, the collar would seem either plesiomorphic or homoplastic for at least two species groups of *Colostethus*. The nature of broken collarlike markings of the two known specimens of *sanmartini* cannot be easily assessed without more material (see discussion and illustration in Rivero et al., 1986). The relationships of Rivero’s *oblitteratus* also clearly should be considered, as should non-Venezuelan species (fig. 15A) that have collarlike markings.

It is not our intent to try to consider possible relationships among these or other collared *Colostethus*, which are being studied by La Marca (ms). Comparisons of a sampling of these species with *Aromobates*, however, is essential, inasmuch as small size, lack of a throat collar, and the probable synapomorphy of lost palatine bones seem to preclude most other *Colostethus* as being closely related to the new frog.

**THROAT COLLAR:** Collars are shown in figures 15–17 and 18B for six species of *Colostethus*, which are to be compared with the situation in *Aromobates* as described herein and shown in figures 4 and 18A. Leaving aside considerable variation in details of the marking, the *Colostethus* agree uniformly in having the collar *at least as well defined in adult females as in males*; the collar is primarily a female character in such species as *C. neblina* (fig. 16; Test, 1956: 2) and *C. guatopoensis* (Dixon and Rivero-Blanco, 1985: 178–179), being weaker or absent in males. The contrasting collar on a bright yellow throat evidently serves a visual function in throat display, especially in female aggressive behavior, as described for *C. collaris* (Durant and Dole, 1975), *C. herminae* (as *trinitatis*: Test, 1954; fig. 1A in Wells, 1980), and *C. trinitatis* (Wells, 1980). Male ventral displays (Dole and Du-

<sup>13</sup> The six species of collared *Colostethus* treated in Edwards (1974) fall out in two groupings in his phenograms (figs. 9, 10). In each phenogram, one grouping includes *collaris*, *olmonae* (then unpublished), and *riveroi* and the other includes an unpublished species name plus *herminae* and *trinitatis* (misspelled “*trinitatus*” throughout this work). The species *dunni* and *meridensis*, both incorrectly considered by Edwards to be collared species, fell out near the first group above—but his concept of these two species may have been based on misidentified material (see original descriptions and also Rivero, “1976” [1978]: 331).

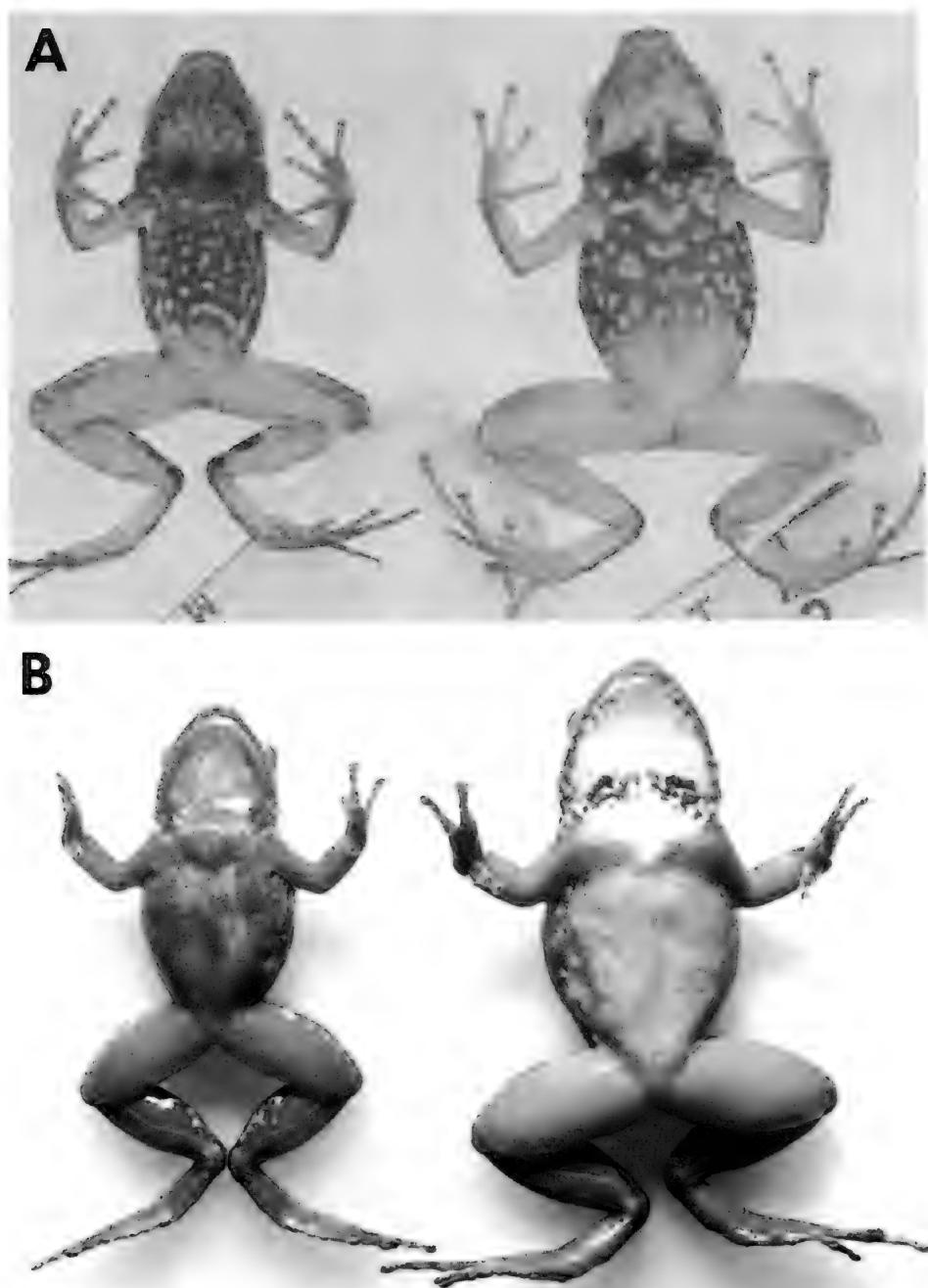


Fig. 15. A. *Colostethus* sp., a species with a collarlike marking from Andean Ecuador (Bolívar-Cotopaxi border: about 7 km airline SSW El Corazón, 800 m). Left to right, adult ♂ (AMNH 104833) and adult ♀ (AMNH 104825),  $\times 2.4$ . B. *Colostethus* sp., cf. *collaris*, a collared species from Andean Venezuela (Trujillo: about 2 km airline W La Peña, 1920 m). Left to right, adult ♂ (AMNH 129982) and adult ♀ (AMNH 129981),  $\times 1.7$ , photographed before preservation.

rant, 1974; Wells, 1980) involve in some species an overall darkening of all ventral surfaces in which the collar is less distinct or absent (figs. 15B, 17A, B).

The sexual dimorphism of the collar is reversed in *Aromobates*, in which females typically lack a collar and males usually have a weak one. Different social behavior in this species is thus expected, but whether the usually vague collar is homologous with any of those in *Colostethus* remains a question. Symplesiomorphy seems likely if all collars are judged homologous.

**BODY STRIPES:** *Aromobates* appears to be symplesiomorphic with various *Colostethus* in having in its variation pale dorsolateral stripes as well as incomplete oblique lateral stripes. Although these markings are variably present and weak in *Aromobates* (fig. 3), their shared presence here and in some *Colostethus* (e.g., table 2) and a few *Epipedobates* suggest that this is the primitive condition, and that either marking alone is derived.

**SIZE:** Dendrobatids are small frogs, generally less than 30 mm SVL, although a few scattered derived species reach maximum female sizes of 45–50 mm SVL (*Epipedobates trivittatus*, *Phyllobates terribilis*, *Dendrobates azureus*, *D. tinctorius*); females of several other species may exceed 40 mm SVL. Among nontoxic dendrobatids, only two species of Venezuelan collared *Colostethus* exceed 40 mm SVL: *Colostethus riveroi* (see Appendix) and *Colostethus guatopoensis* (Dixon and Rivero-Blanco, 1985) both attain a maximum female size of about 44 mm SVL, although *riveroi* is larger on average by several mm.

*Aromobates nocturnus* is a much larger frog (table 1), with even males attaining a larger size (52 mm) than females of any of the above dendrobatids. At a maximum of about 62 mm SVL, female *Aromobates* are 24–37 percent longer than the largest alkaloid-producers mentioned above and 41 percent longer than the biggest *Colostethus*. Mean size in male *Aromobates* is 32–47 percent larger than mean size in male *Colostethus riveroi* and *C. guatopoensis*, respectively, and mean female size is 38–54 percent larger. Thus, the size gap is substantial. “Large” *Aromobates* nonetheless are still small frogs (fig. 1 is about life

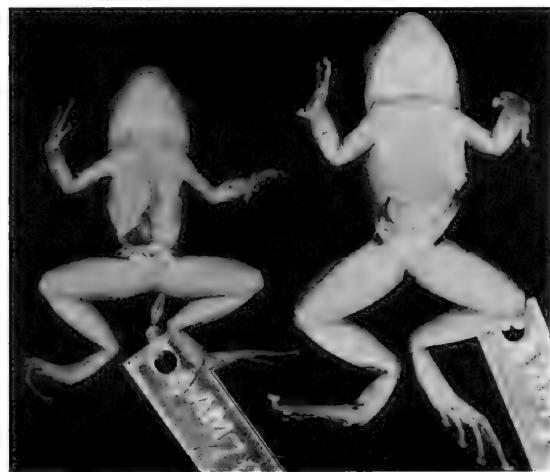


Fig. 16. *Colostethus neblina*, a collared species of restricted range in northern Venezuela (Aragua: Rancho Grande), where it occurs sympatrically with *C. herminae*. Left to right, adult ♂ (AMNH 70758) and adult ♀ (AMNH 70759),  $\times 1.1$ . The narrow dark collar is weak or absent in males.

size); we suspect that “larger” is more primitive than “smaller” in specific lineages of dendrobatids and that miniaturization is derived, although this conclusion is tenuous at best.

**FOOT MORPHOLOGY:** Some degree of foot webbing is widespread in *Colostethus* and almost certainly plesiomorphic, although only a few species including *agilis*, *choocoensis*, and *nexus* (figs. in Frost, 1986; Lynch and Ruiz-Carranza, 1985; Myers, 1991) have webbing that can be described as “extensive.” The few Venezuelan species that have extensive webbing (table 2) seem distantly related to any of the above and include the collared *guatopoensis* and *oblitteratus*, which, according to illustrations in the original descriptions, have the feet nearly as extensively webbed as *Aromobates*. We have not seen either of these possibly conspecific taxa (see footnote 11), but Dixon and Rivero-Blanco (1985) made a good case for considering the weaker webbed *C. riveroi* as the closest relative of *guatopoensis*. Donoso-Barros (“1964” [1965]: 486) mentioned the presence in *C. riveroi* of “three flat metatarsal tubercles,” the extra (median) occurring also in *C. oblitteratus* (Rivero, 1984, fig. 1D) and in

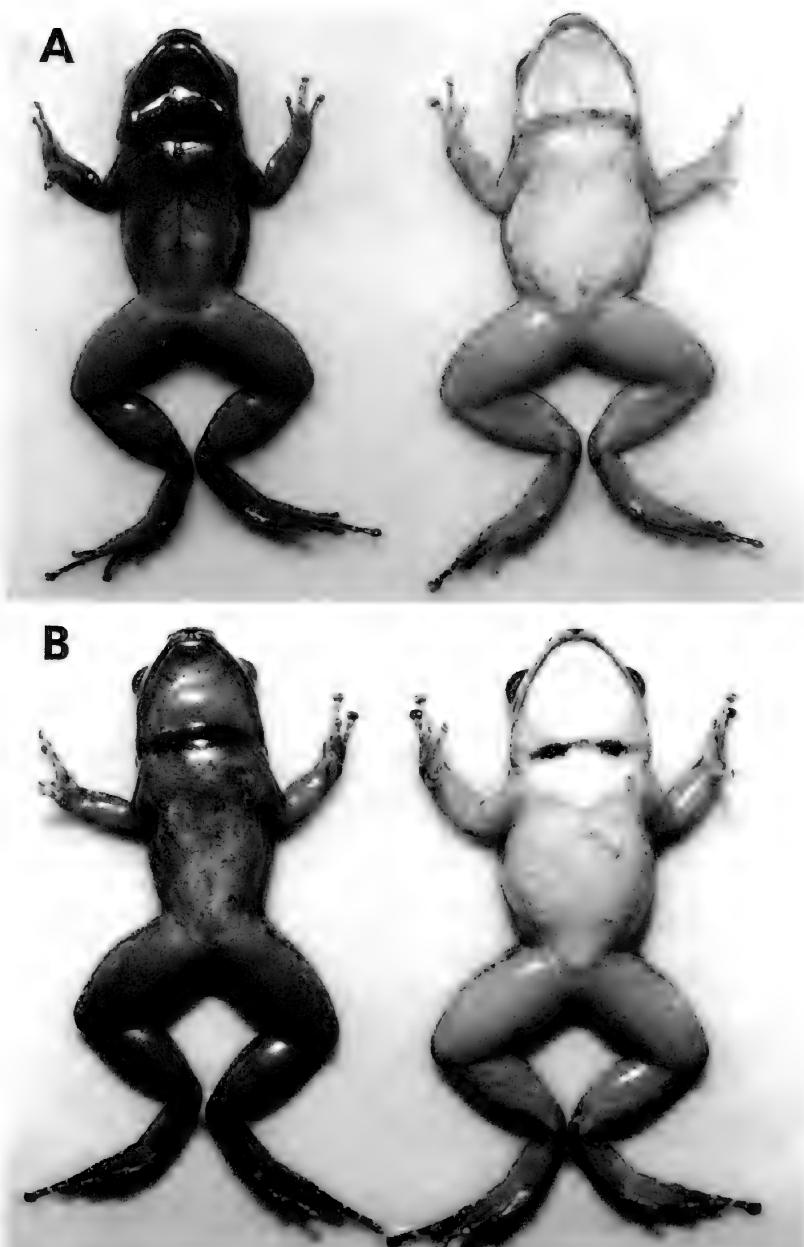


Fig. 17. Collared *Colostethus*, photographed before preservation. A. *C. trinitatis* from Trinidad (13 km NNE Port-of-Spain, 300 m). Left to right, adult ♂ (AMNH 87373) and adult ♀ (AMNH 87377),  $\times 1.8$ . B. *C. olmonae*, paratypes from Tobago (hills above Man-of-War Bay, 1.5–3.5 ENE Charlotteville, 5–100 m). Left to right, adult ♂ (AMNH 87361) and adult ♀ (AMNH 87362),  $\times 2.1$ .

*Aromobates* (fig. 2). This tubercle, virtually ignored in dendrobatid literature except where buried in an isolated description, is, when present, usually less well defined than the ubiquitous inner and outer metatarsal tubercles and is often easy to overlook. The taxonomic distribution is uncertain, but the tu-

bercle does appear in other *Colostethus* and in some *Epipedobates* (fig. 19) and its occurrence in *Aromobates* therefore is judged as symplesiomorphic.

**JAW MUSCLES:** The m. adductor mandibulae externus superficialis (sensu Starrett, 1968) of *Aromobates* is the first report of this

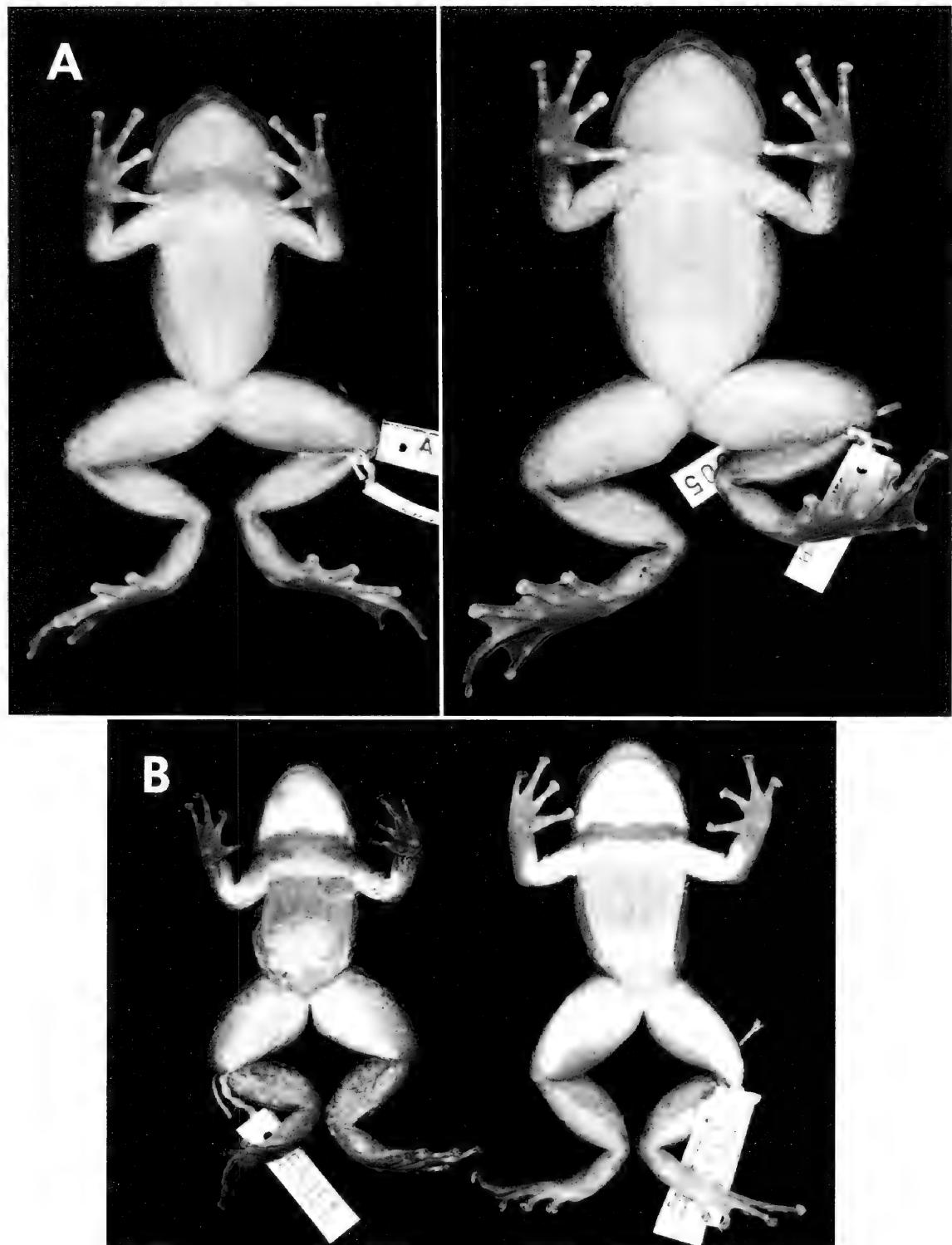


Fig. 18. Venezuelan dendrobatids shown  $\times 1$ . A. *Aromobates nocturnus*. Left to right, adult ♂ (AMNH 130006, paratotype) and adult ♀ (AMNH 130005, holotype). As shown here, the throat collar is normally poorly defined in males and absent or very faint in females (see fig. 4 for maximum development of the male collar). B. *Colostethus riveroi*, largest known member of its genus, with collar well-developed in both sexes. Left to right, adult ♂ (155351) and adult ♀ (133057).

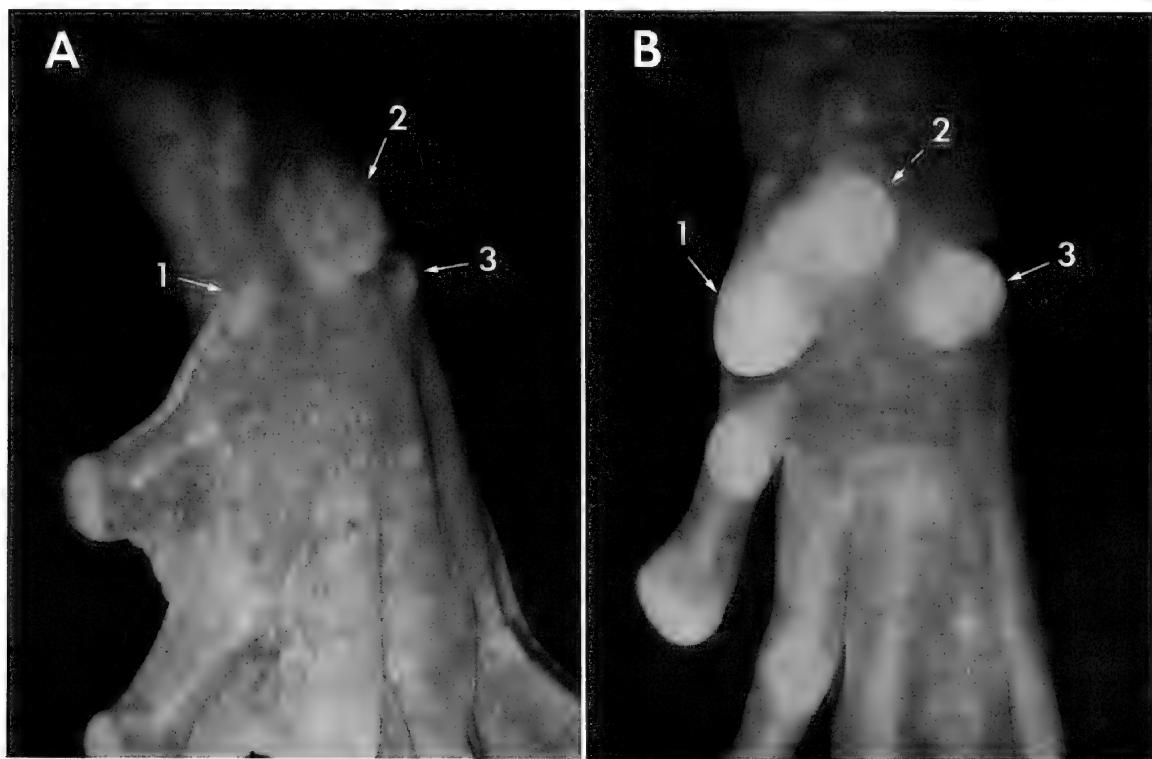


Fig. 19. A. Proximal portion of right foot of *Aromobates nocturnus* (AMNH 130017♀, 61 mm SVL),  $\times 4.8$ , showing maximum development of medial metatarsal tubercle, which is inconspicuous in many specimens. B. Right foot of *Epipedobates trivittatus* (AMNH 91841♀, 44 mm SVL),  $\times 9.6$ , showing occurrence of a median metatarsal tubercle in a distantly related dendrobatid. 1, inner metatarsal tubercle; 2, median metatarsal tubercle; 3, outer metatarsal tubercle.

muscle in the Dendrobatidae. Of 11 skinned *Aromobates* carcasses examined, it was present on 15 of 22 sides (absent in two specimens and present on one side only in three others). The muscle is absent on all 14 sides of seven specimens of *Colostethus riveroi*. The difference between these two species certainly is not likely to be due to chance sampling of a variable character ( $\chi^2 = 13.6787$ , 1 d.f.,  $P < 0.0002$  with Yates correction). Further search among collared *Colostethus* was made by examining jaw musculature (on both sides) in skinned carcasses of *C. sp.*, cf. *collaris* (6 specimens), *neblina* (1), *olmonae* (20), and *trinitatis* (20), and also 20 carcasses of *Colostethus inguinalis*. All these had only the *m. adductor mandibulae posterior subexternus*—the usual dendrobatid condition.

The *m. a. m. externus superficialis* ("E") and *m. a. m. posterior subexternus* ("S") have similar origins and insertions and are identified by the position of the third (mandib-

ular) branch of the trigeminal nerve, which lies medial to the first and lateral to the second (fig. 5). Based partly on ranid ontogenetic development, Starrett (1968) considered presence of both muscles ("S + E") to be primitive leading through loss to two possible derived conditions, namely S or E. A few subsequent students of eleutherodactyline leptodactylids, which are mostly characterized by Starrett's derived conditions, have decided either that: (1) S is primitive and S + E is "intermediate leading to the more highly derived presence" of E (Miyamoto and Tennant, 1984: 766), or that (2) S is primitive and both S + E and E are [equally] derived (Lynch, 1986: 253).

Pending adequate data from suitable out-groups, we follow Starrett's original interpretation and consider as primitive the S + E condition in *Aromobates*, which, considering intraspecific variation, may be in the process of losing the "E" (*a. m. externus superficialis*)

muscle. (However, histological demonstration of separate muscle sheaths, or epimysia, could usefully show if the transformation series truly involves different muscles rather than a labile nerve or single labile muscle.)

**OSTEOLOGY:** Dry and cleared-and-stained skeletal preparations of *Aromobates nocturnus* were directly compared with several cleared-and-stained specimens each of the collared *Colostethus* sp., cf. *collaris* (fig. 15B), *C. riveroi*, and *C. trinitatis*, as well as with *Colostethus inguinalis* and a miscellany of other dendrobatids.

Skeletons of *Aromobates* most generally resemble those of the collared *Colostethus*; strong points of comparison include: the symplesiomorphic presence of palatine bones (long, rodlike structures in all); medial process of pterygoid present (closely approaching or touching otic capsule in *Aromobates* and *C. riveroi*, thinner and shorter in *C. sp.*, cf. *collaris* and *C. trinitatis*); a pronounced preorbital process on pars *facialis* of maxilla; a markedly triradiate squamosal, with the zygomatic (anterior) process as long or longer than retroarticular process of mandible. *Aromobates* differs from the collared *Colostethus* in several characters: it has notably fanglike teeth and seems to have a more heavily ossified pars *facialis* on the maxilla; the anterior ventral edge of the parasphenoid is irregularly serrate in *Aromobates* and in one of three *C. trinitatis*, bifurcate in the other collared specimens; the adjacent (medial) parts of the coracoids are relatively more massive in *Aromobates*; the cartilaginous omosternum of *Aromobates* usually has a small and irregular center of calcification whereas the collared species have a well-defined long bony style; the anterior terminus of the omosternum is Y-shaped in *Aromobates* but nonforked in the others (this end being irregularly expanded in *C. sp.*, cf. *collaris* and *C. riveroi*); the distal ends of the sacral processes are somewhat more dilated in *Aromobates* (fig. 9).

*Aromobates* is not the only dendrobatid with fanglike teeth, inasmuch as the teeth of the much smaller *Colostethus alboguttatus*—a noncollared species < 30 mm SVL—also fit this description (based on dentition examined *in situ* in preserved AMNH specimens).

**SKIN SECRETIONS:** *Aromobates* and *Colos-*

*tethus* s.l. are symplesiomorphic in lacking lipophilic alkaloids (see Daly et al., 1987, for latest review), but *Aromobates* is unique among dendrobatids and rare among anurans (Daly et al., 1987: 1066) in having a vile defensive odor. If present in other dendrobatids and not induced by mere handling as in *Aromobates*, such an odor certainly would be noticed when skinning frogs. Among the collared *Colostethus*, Daly and Myers have skinned six specimens of *C. sp.*, cf. *collaris* and much larger samples of *olmonae* and *trinitatis*. No odor was noticed from these species nor was any reported from *C. riveroi* by S. R. Edwards, who provided six skins of that species for biochemical analysis.

**BEHAVIOR:** Various species of *Colostethus*, including the collared ones, frequent the vicinity of streams where they regularly and purposely enter water for escape behavior or other reasons—but they spend most time on shore. This behavior should be characterized as riparian rather than aquatic. In contrast, *Aromobates* spends most of its time in water and is the only dendrobatid known to us to do so.

A commitment to diurnal habits appears characteristic of virtually all dendrobatids, whereas among other anurans diurnality is a behavioral homoplasy usually occurring at the level of genera or species. There are, to be sure, some secretive dendrobatids that spend their time in dim crevices and are best hunted by day with a flashlight and some that show increased activity during crepuscular periods—and a few otherwise diurnal *Colostethus* (including *C. olmonae* [personal obs.] and possibly other collared species [see Appendix]) extend their long period of diurnal activity into the night. Even so, collared *Colostethus* are easily seen by day on rocks and stream banks, and their visibly complex social lives have therefore been popular subjects for observational studies (Dixon and Rivero-Blanco, 1985; Dole and Durant, 1974; Durant and Dole, 1975; Sexton, 1960; Test, 1954, 1956, 1963; Wells, 1980). Dixon and Rivero-Blanco (1985: 179) noted that *C. guatopoensis* appears “to thermoregulate in patches of direct sunlight . . . One adult male was observed moving around on a streambed boulder in an effort to remain in direct sunlight.”

The clearly nocturnal behavior of *Aromobates* differs markedly from the diurnal habits of dendrobatids generally or of the occasional diurnal to partially nocturnal behavior in a few *Colostethus* (see above). There is a noncollared *Colostethus* (Myers, unpubl.), sympatric with *Aromobates*, that extends its period of daytime activity well into night when there is bright moonlight. But *Aromobates* was active even on the darkest night and apparently not at all by day.

#### PHYLOGENETIC POSITION

As discussed above, *Aromobates nocturnus*—the Venezuelan skunk frog—clearly belongs to the Dendrobatidae, within which it most closely resembles *Colostethus (Hyloxalus)* after the removal of *Colostethus* s.s. *Aromobates* most specifically resembles species of “collared” *Colostethus*, which may not comprise a monophyletic group if Rivero's (1984: 54) assessment of relationships between certain collared and noncollared species holds true. In any case, in *Colostethus* the throat collar is normally as well or better developed in females as in males (at least in the six collared species shown in figs. 15–18) and seems to serve a primary function in female aggressive behavior. *Aromobates* females, on the other hand, have the collar barely perceptible or (usually) lack it altogether, and the male collar is seldom bold. Aside from the collar, other resemblances between *Aromobates* and collared *Colostethus* include relatively large size in a few collared species (to 44 mm vs. 62 mm in *Aromobates*), retention of palatine bones, retention of medial process of pterygoid, and retention of a relatively long zygomatic branch of squamosal (these osteological features tending towards reduction or loss in the Dendrobatidae). The resemblances between *Aromobates* and collared *Colostethus* apparently reflect symplesiomorphy.

*Aromobates* shares with a noncollared Venezuelan species (*Colostethus alboguttatus*) the curious feature of fanglike teeth, but the implications of that character are not evident at this time.

*Aromobates nocturnus* is unique among dendrobatids in its defensive mercaptan or mercaptanlike odor, large size, variable but usual presence of the m. adductor mandi-

bulae externus superficialis, nocturnal habits, and aquatic (vs. riparian) habits. Although probably secreted from the same granular skin glands that produce the dendrobatid alkaloids (Neuwirth et al., 1979; Daly et al., 1987), the presumed organosulfur compound accounting for the vile odor has no parallel in the family. Although it is procedurally proper to consider the intrafamilial unique use of a volatile chemical defense as autapomorphic, a scenario for primitiveness has some attraction (see below). Any of the other unique dendrobatid traits of *Aromobates* might also be special apomorphies, but, pending accumulation of reliable data for suitable outgroups, they may also be primitive for the family. This accords well with other traits judged primitive in the family, including the osteological characters mentioned above, sloping loreal region, and presence (albeit weakly) of both dorsolateral and oblique lateral stripes.

The above analysis necessitates moving certain former familial characteristics up one level, as synapomorphies of *Colostethus* s.l. + the several genera of aposematic dendrobatids (fig. 20). Unfortunately, comparative data for the characters shown in figure 20 are not yet available for the most appropriate outgroups to the Dendrobatidae (Ford, ms) and some character reinterpretation may be necessary as this work develops.

*Aromobates nocturnus* nonetheless seems to be the plesiomorphic sister group of all other dendrobatids. If it is in fact brimming with primitiveness as we suggest, the presence of such a highly derived unique trait as the defensive odor seems anomalous even if theoretically plausible. But what if this or another chemical (nonalkaloid) defense were primitive for the family? It would suggest an explanation for the apparent absence of a chemical defense in *Colostethus* s.l., which itself has seemed anomalous among most amphibian groups (Daly et al., 1987) in possessing normal granular (“poison”) glands (Neuwirth et al., 1979) that produce little or nothing of a noxious quality. The skin of a few or perhaps all species of *Colostethus* are like most frogs in containing small or trace amounts of bufadienolide-like compounds that inhibit  $\text{Na}^+$ - and  $\text{K}^+$ -dependent adenosinetriphosphatase; but, except where secondarily present in high levels in the Bufonidae, such compounds are suspected to serve

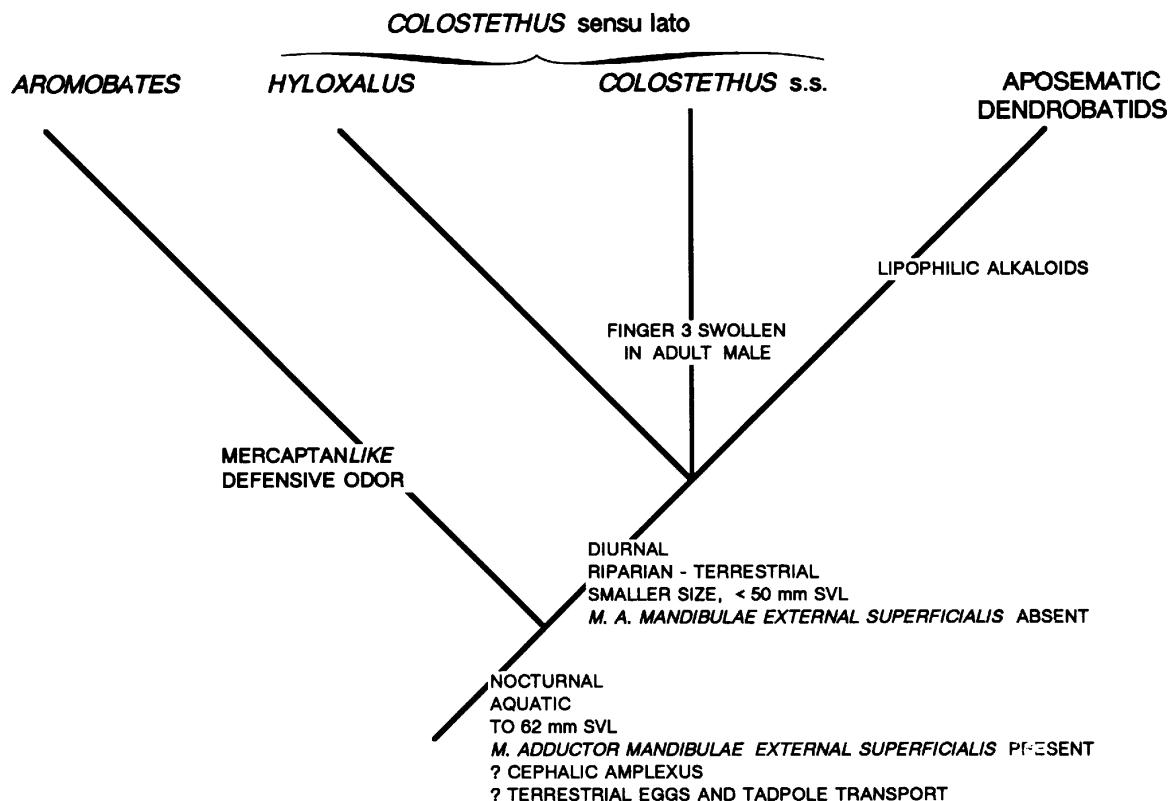


Fig. 20. Influence of *Aromobates* on distribution of selected characters in the Dendrobatidae. Familial synapomorphies that are unchanged by the addition of *Aromobates* are not shown—except for those marked “?” to indicate missing data for the new sister group. Character states uniting *Colostethus* sensu lato with the lipophilic alkaloid-producing group are former synapomorphies for the family that have been shifted one level up. An interesting scenario results if the defensive odor of *Aromobates* is considered primitive rather than derived (see text).

only as physiological regulators for  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase (Flier et al., 1980). So far only one *Colostethus* is known to be toxic (see p. 19).

Although *Aromobates* and *Colostethus* s.l. are clearly symplesiomorphic in lacking the dendrobatid lipophilic alkaloids, the lack of a definitive chemical defense in *Colostethus* s.l. may well be a synapomorphy of loss rather than a condition primitive to the lipophilic-alkaloid lineage as sometimes considered. Perhaps the exquisitely colored “higher” dendrobatids, with their sophisticated alkaloid defenses, had ancestors that were as remarkably offensive as *Aromobates* is today.

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#### APPENDIX: NOTES ON *Colostethus riveroi*

Comparisons of the new Andean frog with the geographically distant *Colostethus riveroi* were considered a priori to be particularly critical, because *riveroi* was described as being partly nocturnal and of exceptional size ("57 mm," which would be about the average size for female *Aromobates*). Some aspects of the original description(s) of *riveroi*, however, require close examination.

*Colostethus riveroi* was discovered and named by the late Roberto Donoso-Barros, who in doing so managed to contribute confusion on several fronts. First there is a dating problem arising from duplicate publication: Authors have attributed the formal description of *riveroi* to "Donoso-Barros, 1964," a paper unfortunately published in a journal whose publication has been consistently delayed. Copies of number 4 ("December, 1964") of volume 4 of the *Caribbean Journal of Science* were hand-stamped with a mailing date of "Oct 13, 1965," which is here accepted. The name "*Prestherapis* [sic] *riveroi* Donoso-Barros," with a validating six-line diagnosis, seems to have been published about nine months earlier, in an obscure

paper dated January 1965 and titled *Nuevos reptiles y anfibios de Venezuela*.

Other amphibian and reptile names seeming to have been published for the first time in Donoso-Barros' first 1965 paper are *Hyla robersimoni*, *Eleutherodactylus lancingii*, *Gonatodes ceciliae*, and *Gonatodes seigliei*. Erroneous (later) "original" citations to these names can be found in the standard compilations by Duellman (1977), Frost (1985), and Peters and Donoso-Barros (1970). As may be gathered by the last citation, Donoso-Barros ignored his earlier paper, which has been mentioned by few (if any) authors other than Vanzolini (1978: 206), who calls attention to other instances of duplicate publication by Donoso-Barros.

In both of Donoso-Barros' descriptions of *Colostethus riveroi*, a size of "57 mm." is given in the diagnosis, but, in the second, longer paper (Donoso-Barros, "1964" [1965]), actual measurements are provided only for a single frog of 44 mm snout-vent length (presumably, but not explicitly, the holotype). But close reading of this paper reveals that 57 mm is the length not of a frog but of a tadpole ("20 mm. body, 37 mm. tail")!

Nonetheless, this species is the largest known *Colostethus*, with maximum recorded snout-vent sizes of 38.4 mm ( $\bar{x} = 36.7$  mm in 5 ad. ♂) and 43.9 mm ( $\bar{x} = 41.7$  in 13 ad. ♀) according to Edwards (1974, table 1), who, with Juan León, collected a large series ( $N = 33 +$  tadpoles) of *riveroi* at the type locality in May 1970.

Donoso-Barros had only five specimens in his type series and he probably had little basis for his unelaborated statement ("1964" [1965]: 489) that "*P. riveroi* is more active [than sympatric *trinitatis*] at night." It is entirely conceivable that Donoso-Barros did see specimens at night, but Edwards' fieldnotes on file at the University of Kansas Museum of Natural History indicate that all his specimens were found by day in and along a cascading stream bed. Therefore it seems at least primarily diurnal as expected from knowledge of related species (see section on Behavior under Comparisons with "Collared *Colostethus*").

The dorsal drawing of an unidentified specimen (holotype?) of *riveroi* (Donoso-Barros, "1964" [1965]: 487) is a perhaps misinformative representation of the species' normal pattern in that it depicts a light dorsum with pronounced dorsolateral dark and pale stripes. Edwards' fieldnotes (and the preserved specimens) indicate: "dorsum solid brown, ♂♂ darker brown, lacking dorsolateral or ventrolateral stripes. Irregular darker brown dorsal blotches in ♀♀. . . . Indistinct lateral oblique line yellow, from groin to above arm." In a few preserved specimens (e.g., KU 133066), however, there is a discernible but ill-defined dorsolateral

stripe of pale brown additional to the lateral stripe. Edwards noted that in life the throat is bright yellow in females, with a yellow area behind the throat collar and with yellow patches on the belly and undersides of the thighs (in general agreement with the orange areas described by Donoso-Barros) but that males have gray throats and chests, with reduced yellow on belly and thighs.

The type series of *Colostethus riveroi* originally was in Donoso-Barros' private collection; the present location of the holotype is not known to us. Comparisons with *Aromobates* in the present pa-

per were based on the following specimens of *riveroi* collected by the Edwards party (AMNH specimens were obtained on exchange from the University of Kansas Museum of Natural History, where most of the material was deposited). *Specimens Examined*: Venezuela: Sucre: Cerro Azul, 600 m, 10 km N Macuro, AMNH 134141, 134145–134146, 134142–134144 (cleared & stained skeletons), KU 133049–133050, 133055–133056, 133061–133063, 133065–133069, 133074–133078, 133165, 133171, 155347, 155349, 155354.





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